A General Consideration of the Subaërial and Fresh-water Algal Flora of Ceylon. A Contribution to the Study of Tropical Algal Ecology. Part I.—Subaërial Algæ and Algæ of the Inland Fresh-waters.

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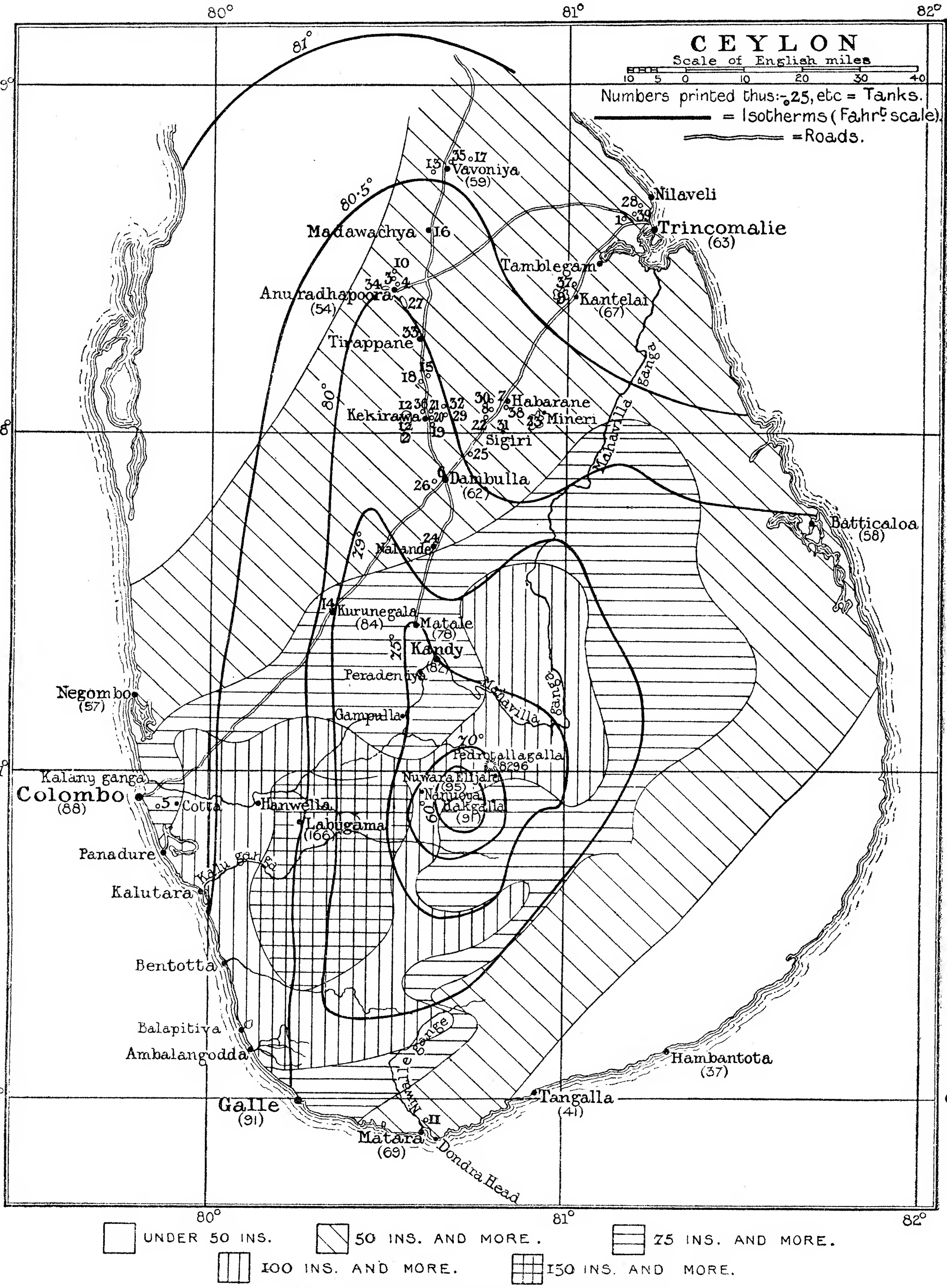
(Communicated by Professor F. W. Oliver, F.R.S.,—Received June 26,—Read November 1, 1906,—Received in revised form, January 2, 1907.)

Introductory Remarks.

During the year 1902 I was occupied with a study of the algal flora in the hot-houses of the Royal Botanic Gardens at Kew, and certain observations made then seemed scarcely to support the prevalent view of the very close similarity between tropical and temperate algal vegetation. This stimulated me to undertake a personal investigation of some tropical algal flora, and Ceylon was chosen owing to the diversity of climatic conditions which it presents. My object was rather to study the ecological and biological aspects of the algal vegetation than to make a systematic collection of materials for a flora, and I hope to be able to show that I have been in some measure successful. A careful analysis, as I think the subsequent pages of this paper will show, brings to light very considerable differences between algal growth in the tropics and in our parts, although a certain similarity between fresh-water Algæ all over the surface of the earth (considerably greater than in the case of the terrestrial flora) is indisputable. It is, in fact, a natural consequence of the uniform character of the surrounding medium.

The island of Ceylon is peculiarly favourable for a study of the influence of tropical temperature and moisture on the distribution of algal growth, since the rainfall varies considerably in different parts of the island, while the mountainous southern portion (attaining a height of 8000 feet and more) produces a very considerable range of temperature, from the intense heat of Colombo and other lowland places to the high-lying Nuwara Eliya, where, at certain times of the year, the thermometer falls to below freezing point at night. In fact, we have here confined in a narrow compass almost all the different possibilities that can be realised in the tropics. It may be well at this point to briefly outline the range of variation in this respect (see also the map). The low country, with its high tropical temperature, shows great diversity in the amount of rainfall; so that some localities are exceptionally



AVERAGE ANNUAL RAINFALL.

DESCRIPTION OF THE MAP.

The Map shows the different localities mentioned in the present paper, the distribution of rainfall, and the isothermal lines (after Trimen and Wright). The bracketed numbers placed below the place-names are amount of rainfall in inches. The unbracketed numbers show the position of the tanks, which are as follows :—

1. Andankulam.	14. Kurunegalawewa.	27. Nuwarawewa.
2. Balaluwewa.	15. Madakanawewa.	28. Periyakulam.
3. Balankulam.	16. Madawachyawewa.	29. Punchikekirawa.
4. Basawakkulam.	17. Madokotaikulam.	30. Senadiniyagawawewa.
5. Borlasgamawewa.	18. Mahakadawellawewa.	31. Sigiri tank.
6. Dambullawewa.	19. Mahakekirawa.	32. Tibbotuwawewewa.
7. Habaranewewa.	20. Malawewewa.	33. Tirappanewewa.
8. Hiriwadunnewewa.	21. Mancadawewa.	34. Tissawewa.
9. Lake Kantelai.	22. Megaswewa.	35. Villamkulam.
10. Karambewawewa.	23. Lake Mineri.	36. Walikulam.
11. Kekunadurewewa.	24. Nalandewewa.	37. Wendrenkulam.
12. Kelawewa.	25. Namoluwewa.	38. Yaka-anaguhuwewa.
13. Koilpuliumkulam.	26. Neravieawewa.	39. Kannia Hot Springs.

wet (*e.g.*, Kalutara, Labugama), others (under the prevalent tropical conditions) very dry (*e.g.*, Hambantota, Vavoniya), whilst numerous intermediate conditions between the two extremes are found (*e.g.*, at Colombo, Matara, etc.); the wettest place I visited was Labugama (166 inches). The amount of rainfall at Peradeniya is not much less than at Colombo, but the lower temperature, due to the higher altitude, has some influence on the algal vegetation. In travelling upwards to Nuwara Eliya the gradual change of temperature is very perceptible; the climate in the uplands is indeed practically European, although not so cold in winter, and considerably hotter in the middle of a sunny day (mean annual temperature a little over 60° F.). The rainfall, however, is heavy (about 90 inches), and that produces an abundant vegetation. If we further bear in mind that there is a coastal and an inland region, we shall have roughly reviewed the diversity of climatic conditions obtaining in the island.*

Since my stay in the island was of brief duration (August 21 to November 10, 1903) my account of the algal vegetation is necessarily very incomplete

* My travels in Ceylon may be subdivided into three distinct tours: (i) Along the western and southern coasts as far as Hambantota, the time being devoted to a study of the algal flora and Phytoplankton of the lagoons and estuaries at Negombo, Panadure, Kalutara, Ambalangodda, Bentotta, and Matara, and to an investigation of the subaërial Algæ; (ii) Into the northern plains as far as Vavoniya and Trincomalie, where I was mainly occupied with a study of the Algæ found in the inland fresh-waters (especially the numerous tanks or irrigation-reservoirs); (iii) A brief visit to the uplands round about Nuwara Eliya, which proved particularly interesting in comparison with the observations made in the lowlands. In addition to that, I stayed intermittently at Peradeniya for about a fortnight.

in places. I rarely stayed more than two or three days in any one locality, so that although able to familiarise myself with a wide range of climatic conditions and their influence on algal growth, I was unable to enter into detailed study of any given problem. Moreover, my observations, of course, merely deal with one phase of the algal vegetation, and it is possible that many other peculiarities would come to light if the period of observation could be extended over an entire year. I am, however, inclined to think that algal growth in the tropics will not show so marked a periodicity as obtains in our parts. The rice-fields alone are likely to be interesting from this point of view (see p. 242), since the Algæ in them are exposed to regularly alternating periods of desiccation and inundation. The greater part of my observations were carried out during the dry season, although I remained long enough to see some of the effects of the heavy rains, which begin in November. In many respects I was fortunate in being able to collect during the dry period, since the rains would very soon make access to many of the pieces of water studied exceedingly difficult. The dry season is, moreover, the interesting one from our point of view, for we then have a very essential factor influencing tropical algal vegetation in an acute stage, viz., the risk of desiccation under the burning glare of the tropical sun.

The main purpose of the present paper* is to indicate some of the more important differences between the subaërial and fresh-water algal vegetation occurring in the tropics and that found in temperate regions, and also to point out the essential variations in tropical algal vegetation under the influence of diverse external conditions. Most of those who have written on the subject of algal vegetation in the tropics—and the literature is practically confined to a few short introductory remarks in the systematic floras—have emphasised its similarity to that of temperate regions,† and little or no attempt has been made at determining the differences; this is mainly due to the fact that most of the works on tropical fresh-water Algæ are the outcome of casual, and on the whole, probably very unrepresentative collections by botanical travellers whose main interest lay in other directions. No one, as far as I am aware, has

* A large part of the expenses of the present investigation were covered by a grant from the Government Grant Committee of the Royal Society, to whom I am much indebted for the help thus afforded to me. I also take this opportunity of heartily thanking all those who were kind enough to assist me in the course of these investigations, either by their extensive hospitality or by direct help during the performance of the work. I wish especially to return thanks to Dr. J. C. Willis, Mr. Carruthers, and Mr. Wright, of Peradeniya, to Mr. K. Bamber and Dr. A. Willey, of Colombo, to Mr. Nock, at Hakgalla, and Mr. Lewis, of the Forest Department. The entire illustration of this paper has been carried out by my wife.

† *Cf.*, for instance, Lemmermann, "Üb. die v. Herrn Dr. Volz auf seiner Weltreise gesammelten Süsswasseralgen," 'Abh. Nat.-Ver.,' Bremen, vol. 18, 1905, p. 143 *et seq.*

attempted to study the subject from the point of view put forward in the present communication.* My object is thus to outline the general features of distribution and biology, and I have rarely spent much time on specific determinations. They would in most cases be quite valueless from the present point of view, and would, moreover, have very considerably delayed publication; and it seemed well to write this general paper before one's recollections and impressions of the aspect of the algal flora had become dimmed by the lapse of a longer period than has already passed since the work was undertaken. Certain subjects, which are dealt with quite briefly in the present communication, will be considered more fully later on. I hope ultimately to be able to publish a complete systematic list of the Algæ present in my Ceylon collections, although I prefer to postpone such a publication until I have had opportunities of further study of tropical algal floras.

Consideration of the Algal Flora.

The following special considerations are subdivided as follows:—

(*a*) Subaërial Algæ, *i.e.*, those growing on trees, stones, walls, etc. (character and distribution dependent mainly on temperature, moisture and degree of shading):—

(i) The lowland vegetation (p. 203).
(ii) The upland vegetation (p. 215).

(*b*) Algal vegetation of the inland fresh-waters (character and distribution dependent mainly on temperature, aeration and composition of water):—

(i) Algæ of the tanks and other large inland masses of fresh-water (p. 218).
(ii) Algæ of roadside ditches and pools in the lowlands (p. 233).
(iii) Algæ of marshes and padi-fields (p. 241).
(iv) Algæ of rock-pools (p. 242).
(v) Algæ of wells and springs, *i.e.*, aerated, but standing water (p. 250).
(vi) Algæ of the small pools of the uplands (p. 252).†

This subdivision is in great part artificial, but it will be found that the character of the algal growth in many of the collections of water mentioned is on the whole sufficiently different to make such a separation useful. It must, however, be pointed out, that in the case of Algæ the delimitation of distinct

* Bohlin, in his 'Étude sur la flore algologique d'eau douce des Açores,' gives a somewhat analogous account of the algal flora of the subtropical Azores.

† The second part of this paper, which I hope to publish in the course of the year, will deal with the Algæ of flowing water (rivers), and of the lagoons and river-estuaries, and with the Plankton.

formations, except as regards the two fundamental groups of marine and fresh-water Algæ, is by no means so marked a one as in the case of the terrestrial higher plants. It is often, only by a study of extreme cases, that we can draw any definite limits between one kind of algal vegetation and another, for generally numerous intermediate types are to be met with. Algæ, and probably water-plants generally, are much more plastic than terrestrial plants, and many forms of aquatics are no doubt capable of adapting themselves to a variety of modifications in their environment. But there are also amongst the Algæ certain forms which are much more susceptible than others to such variations in their environment, and which are therefore of more limited distribution, and these are the forms which will characterise certain prevailing conditions in the surrounding medium. They are the character-plants, which will help us to determine our aquatic formations, and it is requisite to study them primarily, and to determine the exact conditions which influence their presence or absence. Other species will then be found to be almost constantly associated with these character-plants, and will make up the subordinate members of the formation. Whereas amongst terrestrial plants each formation probably always has one or more character-plants, which occur in this formation only, and are absolutely distinctive of it, aquatic formations will often lack so emphatic a character; they will probably in many cases be distinguished by the way in which the different members of the formation grow together, rather than by any individual species. It even seems quite possible to imagine two algal formations of almost identical specific composition, but differing from one another biologically or physiologically; as far as I am aware, such formations are not known to occur amongst terrestrial plants.

The preceding remarks are intended to indicate the scope for research in the field of aquatic ecology, a subject on which practically nothing is known at the present day, but the importance of which it is well to recognise at the outset of considerations like those with which we are dealing. We are almost entirely ignorant of the true factors which lead to the development of certain algal forms in one piece of water and of others in a second. Certain preliminary researches on this subject, which have been undertaken in the past years on the British fresh-water algal flora, have given a number of interesting results; some of these have been dealt with at another place, where the subject of algal formations, briefly touched on above, is considered in greater detail.* My time in Ceylon was, of course, far too limited to admit of collecting more than a few meagre observations on possible tropical fresh-water formations. Moreover it is quite impossible to fully characterise an

* See Fritsch, "Problems in Aquatic Biology, with Special Reference to the Study of Algal Periodicity," 'New Phytologist,' vol. 5, 1906, p. 149 *et seq.*

algal vegetation unless it has been studied, at least, throughout the course of an entire year. So much seems probable, however, that a large number of the algal formations of the tropics are quite different to those of our parts, although certain of them may possibly be parallel in their nature (*cf.* especially p. 240). On the whole, Phanerogams seem likely to be of more importance as character-plants in the aquatic formations of our parts than in the tropics, where the Algæ will, probably in most cases, prove more distinctive; this suggestion is, however, merely based on recollection of the aspect of the fresh-water flora of the tropics, and careful investigation may quite disprove it.

(a) *Subaërial Algæ.*

A consideration of the subaërial algal flora affords a good illustration of the existence of important differences between tropical and temperate algal vegetation.

(i) *The Lowland Vegetation.*—The first impression of an algologist after landing in Colombo, which combines tropical heat with a fairly considerable rainfall (88 inches), is the abundant algal covering on the walls of the houses, on rocks, on exposed tree-trunks, etc. A rich growth of Algæ on surrounding objects is characteristic of every really moist locality, but it is only when heat and moisture combine that we get so luxuriant a growth as in the tropics; moreover, a few minutes' walk about Colombo is sufficient to convince one that the composititon of this algal growth is one quite unlike that of temperate regions. One sees practically nothing of the *Pleurococcus, Hormidium,* etc., so characteristic as epiphytes in our climates, green Algæ being very inconspicuous in all exposed situations (excepting *Trentepohlia, cf.* below). Isolated colonies of green unicellular forms are occasionally to be found in very subordinate amount amongst unicellular Cyanophyceous (adhesive) growth, but pure green coatings are completely wanting. There are very few records in the literature of the occurrence of green subaërial Algæ in the tropics* (chiefly *Pleurococcus crenulatus,* Hansg., *P. Kützingii,* West, and *P. vulgaris,* Menegh., *Hormidium murale,* Kütz),† and none of these records give us any idea of the quantity in which these species occur; nor is it possible in the absence of accurate descriptions of the habitat, to estimate the special conditions under which these forms appear in the tropics.

The subaërial‡ Algæ of the tropics nearly all belong to the Cyanophyceæ

* Regarding terrestrial forms of *Vaucheria,* see p. 217.

† The existing data as to the composition of algal growth in the tropics are discussed more fully elsewhere ('Annals of Botany,' vol. 21, No. LXXXII, April, 1907, p. 239 *et seq.*).

‡ The term "subaërial" algal flora is used to denote all those forms not actually growing in water. Epiphytic Algæ constitute those growing on parts of other plants (trunks of trees, leaves, etc.), lithophytes are those growing on rocky surfaces.

(Myxophyceæ) and, owing to this characteristic composition, the algal covering is for the most part of a much more sombre hue than the bright green one of our parts. This dark colour is only relieved here and there by an occasional brighter patch, due either to a growth of Mosses, which, however, do not apparently prosper very well in unsheltered situations, or to the thin bright blue-green coating of an *Oscillaria,* or of some member of the Chroococcaceæ (*sensu* Kirchner), which are often able to obtain a foothold on very smooth walls, etc., which are unsuitable substrata for other forms. *Trentepohlia,* with its reddish-yellow tufts, also forms a relatively frequent and agreeable interruption to the dark Cyanophyceous growth.

Subsequent considerations (*cf.* p. 224, *et seq.*) will show that the blue-green Algæ play a far more important part in the tropics than they do with us, and a tropical fresh-water or subaërial* algal flora obtains its stamp from the prevalence of this group. In order to realise the extent of development of the subaërial Cyanophyceæ in the tropics, it is necessary to pay a visit to a damp hot-house,† or to some hot spring,‡ where conditions of a similar nature prevail. Here also we find the green Algæ crowded out and superseded by the blue-green forms.

Most of the Cyanophyceæ require two factors for abundant development; the first is plenty of moisture, the second a sufficiently high temperature. These two factors determine the distribution and character of the blue-green subaërial growth. The importance of the former factor is, of course, perfectly obvious without much comment; it is also manifest in comparing the moist

* The only reference I am aware of that speaks of an abundant occurrence of subaërial Cyanophyceous growth in tropical regions is one by Welwitsch ('Journ. Travel and Nat. Hist.,' vol. 1, 1868, pp. 22—36), on "The Pedras Negras of Pungo Andongo in Angola." The author describes the prolific growth of a species of *Scytonema* on the upper portions of the mountains, and also refers to another species (*Porphyrosiphon Notarisii*) as covering the sandy soil in the valley of the Cuanza River for considerable stretches (*cf.* also West and West, in 'Journal of Botany,' vol. 35, 1897, p. 303; and Warming, 'Ökol. Pflanzengeogr.,' German Edit., Berlin, 1896, p. 215).

† *Cf.* Fritsch, "Algol. Notes, IV.—Remarks on the Periodical Development of the Algæ in the Artificial Waters at Kew," 'Annals of Botany,' vol. 17, No. LXV, 1903, p. 274; also "Algæ," in "The Wild Fauna and Flora of the Royal Botanic Gardens, Kew," 'Bull. Miscell. Inform. Roy. Bot. Gards., Kew,' Addit. Series V, 1906, p. 187 *et seq.* In the *Nepenthes*-house at Kew the blue-green Algæ even settle down on the leaves of the cultivated plants (*cf.* also Schmidle, "Epiphylle Algen," etc., 'Flora,' vol. 83, 1897, p. 323 *et seq.*).

‡ See G. S. West, "On some Algæ from Hot Springs," 'Journal of Botany,' vol. 40, 1902, pp. 241—248; W. H. Weed, "Formation of Travertine and Siliceous Sinter by the Vegetation of Hot Springs," 9th Ann. Rep. U.S. Geol. Survey, 1887—88, p. 619 *et seq.*; and F. Cohn, "Ueber die Algen des Karlsbader Sprudels," etc., 'Abh. Schles. Ges. Vaterl. Cultur,' 1862, p. 35 *et seq.* The vegetation in such springs is almost entirely composed of Cyanophyceæ and Diatoms (see also Sect. *b* (v), of the present paper, p. 251).

lowlands of Ceylon with the drier regions having a lower rainfall. Thus at Matara, on the south coast, and at Dambulla, in the Central Province, the decrease in the extent of the algal covering is very marked; whilst in still drier localities (*e.g.*, Hambantota and Negombo, on the coast, Anuradhapoora, in the North Central Province), houses, rocks, etc., are practically clear of any growth (or only bear small Mosses and Lichens), except in particularly favourable positions. On the other hand, the heavier the rainfall at any locality, under the same conditions of temperature, the more abundantly is the blue-green element developed; the best example of this that I met with was at Labugama (166 inches), where every available object is clothed with blue-green forms. The importance of moisture is also well illustrated in the colonisation of rugged vertical surfaces, since at first only the projections, which are the points about which moisture mainly collects, become occupied by Cyanophyceous growth.

The importance of a high temperature is also easily recognised. A visit to a wet greenhouse in our regions, which is kept at a relatively low temperature, shows us that here green Algæ and Mosses are the more successful elements in the subaërial vegetation, whilst the Cyanophyceæ, where developed, present a different aspect; compare, for instance, the growth in the Temperate and Tropical Fern Houses at Kew. The same observation can, in some respects, be made in Ceylon, as we go higher and higher up the central mountain range to Nuwara Eliya (see the discussion of the subaërial Algæ of the uplands).

Though temperature and moisture are in all probability the determining factors in the distribution of the subaërial Cyanophyceæ within the tropics, this group is provided with certain biological features, which must be regarded as peculiarly suited to the dominant factors of the environment, and enable it to exist so well under the prevailing conditions. In the first place there is a well-marked alternation of a wet and dry period,* which the Cyanophyceæ are well adapted to withstand, owing to the strongly developed mucilage investments, which are so prominent a feature of the group, and which enable them to withstand prolonged drought.† In this relation, it is interesting to notice that forms with a sheath of semi-liquid diffluent

* See J. C. Willis, "The Royal Botanic Gardens of Ceylon as a Centre for Botanical Study and Research," 'Annals. Roy. Bot. Gards., Peradeniya,' vol. 1, 1901, p. 17 *et seq.*; also "Studies in the Morphology and Ecology of the Podostemaceæ," *loc. cit.*, vol. 1, Part 4, 1902, pp. 278—279.

† Hansgirg, "Ueber *Bacillus muralis*, Tomaschek, nebst Beiträgen zur Kenntnis der Gallertbildungen einiger Spaltalgen," 'Bot. Centralbl.,' vol. 35, 1888, pp. 54, 102; B. Schröder, "Untersuchungen über Gallertbildungen der Algen," 'Verhandl. Nat.-Med. Ver. Heidelberg,' New Ser., vol. 7, p. 183 *et seq.*, especially p. 185.

mucilage are far commoner in the uplands than in the lowlands, where the risks of desiccation are much greater (see also below).* Secondly, we find the subaërial growth of Cyanophyceæ developed in situations which are often exposed to a strong light and the presence of a second colouring matter (phycocyanin) side by side with the chlorophyll, undoubtedly suits them to an existence under such conditions. The presence of this additional pigment shifts the assimilation-maximum,† but the phycocyanin, no doubt, also acts as a kind of screen to the chlorophyll, although the exact *modus operandi* remains an open question. The great variety presented by the colour of the cell-contents in the Cyanophyceæ is familiar to all, yet we know practically nothing about the meaning of these diverse shades of pigmentation. Gaidukov‡ has experimented with *Oscillaria* from this point of view, and has shown that the colour assumed by the cell-contents is complementary to that of the supplied light, and that variation of the colour of the latter induces corresponding changes in the colour of the *Oscillaria*-filaments. So that in addition to the screening action§ of the phycocyanin it probably plays some other important part in adapting the blue-green group to varying types of illumination. The absence of any protective pigment is, no doubt, one of the main causes of the lack of green algal forms in the subaërial vegetation, although the rapid growth of the hardy blue-green element certainly contributes very considerably to crowd them out. Mosses and Liverworts are also mostly wanting in localities exposed to the strong light, although they get on well enough as epiphytes on the tree-trunks in the moist shady jungles and forests. It is interesting to notice in this connection that the only member of the green Algæ, which really competes successfully with the

* *Cf.* also Gomont, "*Myxophyceæ hormogoneæ*" (in J. Schmidt., "Flora of Koh Chang"), 'Bot. Tidsskrift.,' vol. 24, 1901–2, p. 203. He remarks: "Si l'on examine le catalogue que nous en donnons, on s'aperçoit immédiatement que les Algues à gaînes épaisses et colorées l'emportent de beaucoup par le nombre des espèces et par leur fréquence. Ainsi, tandis que les genera *Oscillatoria*, *Lyngbya*, *Phormidium*, *Hydrocoleum*, ne sont representés chacun que par une espèce, les *Scytonema* et *Stigonema* en renferment treize à eux seuls . . . cette absence n'est pas purement accidentelle, mais, ainsi qu'on l'a maintesfois observé, les plantes les mieux adaptées aux régions tropicales sont celles qui trouvent dans l'épaisseur, la consistance ou la coloration de leur gaîne une protection contre les sécheresses fréquentes et l'intensité de la lumière."

† See Pfeffer and Ewart, 'The Physiology of Plants,' vol. 1, Oxford, 1900, pp. 343—344.

‡ "Über den Einfluss farbigen Lichts auf die Färbung lebender Oscillarien," 'Anhg. z. Abh. Kgl. Preuss. Ak. d. Wissensch.,' 1902; "Weitere Untersuchungen über den Einfluss farbigen Lichts auf die Färbung der Oscillarien," 'Ber. Deutsch. Bot. Ges.,' vol. 21, 1903, p. 484 *et seq.*

§ In many cases the cell-contents no doubt obtain additional protection from the intense light in the sheaths of the filaments, which are very frequently brown, yellow, or red in colour. The colour of the sheath is also subject to much variation (*cf.* the first footnote on this page).

Cyanophyceæ in exposed situations, is the genus *Trentepohlia;* the latter, as is well known, is characterised by the presence of hæmatochrome in its cells, and this probably also has a protective function against too intense illumination. Such an interpretation is suggested by the fact that the colour of the filaments varies according to the intensity of the light, being more or less green where shaded, and yellow to yellowish-red in the full light.* Species of this genus are particularly common on the trunks of the cocoanut trees in the plantations along the sea shore and on embankments by the roadside.†

The subaërial Cyanophyceæ in Ceylon exhibit a number of different modes of growth, which are, no doubt, of the nature of adaptations to special external conditions. My stay in the island was not sufficiently prolonged to make it possible to analyse these conditions satisfactorily, but I am able to put forward a number of probable suggestions regarding the factors favouring the one or other mode of growth. The simplest and one of the commonest habits assumed by the subaërial blue-green element may be styled the "adhesive" mode of growth, the Alga being firmly adpressed to the substratum; this occurs in all the gelatinous‡ and encrusting unicellular forms (*Aphanocapsa, Aphanothece, Glœocapsa, Chroococcus,* etc., fig. 1, B and D), and also in certain of the filamentous genera (*Nostoc,* a few species of *Calothrix, Oscillaria, Hypheothrix, Lyngbya,* especially the section *Phormidium*). On the whole this type of growth rarely attains considerable thickness, a result probably of the difficulties of interchange of gases in the inner layers of the stratum. The only well-marked exception is the genus *Phormidium,* but here the inner portions of the often thick lamellæ merely consist of empty sheaths, while only the outer parts contain living filaments. The forms exhibiting the adhesive mode of growth are the first successful colonists of new ground, and are especially adapted to grow on smooth surfaces, where they often form a very thin, slippery film.

A second type of growth may be described as the "tangled" one; this (like the remaining two) is confined to the filamentous forms, and is due to the fact that the filaments are bound together in bundles, which are irregularly interwoven with one another, much as in many of the submerged filamentous Algæ. The denseness of the tangles varies very considerably. In the majority of cases, this growth was found to be relatively thin (although generally

* See also the statements on p. 248 of Oltmanns' 'Morph. u. Biol. d. Algen,' vol. 1, Jena, 1904.

† Species of *Trentepohlia* may become epiphyllous, like some of the Cyanophyceæ. I did not observe any such cases in Ceylon, although that is probably due to the small amount of time at my disposal. Other Chroolepideæ are permanent leaf-epiphytes.

‡ It should be pointed out, however, that these gelatinous forms are rather rare in the lowlands, and far commoner in the moist uplands (*cf.* below, pp. 215, 216).

attaining greater thickness than an adhesive growth) before its surface became colonised by other kinds of Algæ (exhibiting tufted growth). In the few cases in which a thick tangled stratum was observed, only the external portion was generally found to be living, the inner part consisting largely of dead sheaths. The tangled type of growth leads to the retention of a considerable amount of air in the interspaces between the filaments, and this is probably of advantage from a respiratory point of view in comparison to the adhesive habit; this suggestion has, however, first to be confirmed by experiment. On the other hand, this mode of growth (like the adhesive one) is not well adapted to the absorption of atmospheric moisture, since only few of the filaments project freely into the air. Such growth is probably largely dependent for its supply of moisture on the substratum on which it grows, and this is in agreement with the fact that it prospers best on clay embankments or porous rock-surfaces. As it gets thicker, it very often passes over into tufted growth (see below and fig. 1, C) or becomes overgrown by the tufted growth of another more successful form.*

The tangled type of growth is met with in subaërial forms of *Tolypothrix, Hapalosiphon, Scytonema, Stigonema,* etc., and in nearly all cases the filaments are provided with firm consistent sheaths. In most of these genera (mainly in *Stigonema minutum,* Hass. ? and species of *Tolypothrix*) one occasionally meets with tangles growing in protected situations, and exhibiting a characteristic association with a film of air which gives their surface a bluish grey or bluish colour and a silvery sheen, and not only occupies the interspaces of the tangles, but covers their entire surface. The forms under consideration seem to avoid direct moisture as much as possible, and grow in situations which are more or less protected from the rain. The air is held so firmly in the interspaces of the tangle that it has not been dislodged by the preserving fluid, but it seems probable that the impact of falling rain-drops would be able to displace it, and that this is the reason why these forms are only found growing in sheltered situations. The species exhibiting this association with air, however, possess another peculiarity in the form of an irregular incrustation on the sheath, completely absent at some points, but forming an opaque covering which obscures the enclosed trichomes at others. In some

* It may be pointed out, however, that both from the point of view of respiration and of absorption of moisture the various species and genera of Cyanophyceæ may differ markedly among one another; thus one form may be much better enabled to withstand the drawbacks of an adhesive or tangled growth than another. That, under certain circumstances, a tangled growth may be laden with moisture is evidenced by the fact that in damp protected localities I occasionally found aquatic Algæ (*e.g.*, species of *Ulothrix*) growing on the surface of the tangle. These Algæ probably obtain the necessary moisture by absorption from the tangle below.

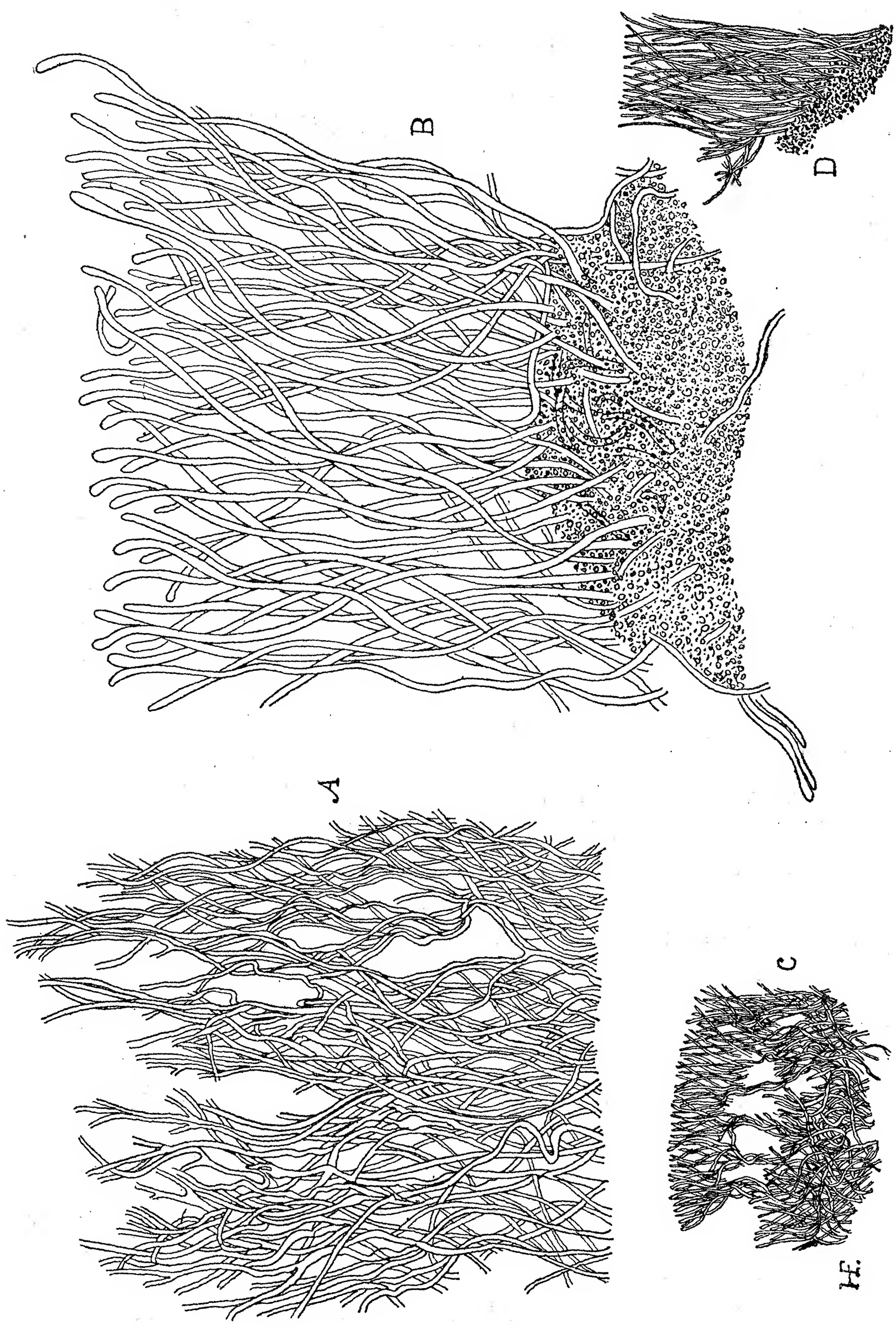


Fig. 1.—Illustration of various Types of Tufted Growth (only the sheaths of the individual filaments are shown). A ($\times 60$).—Rather irregular tufted growth of a *Tolypothrix*. B ($\times 60$).—Tufted growth of a *Tolypothrix*, showing disorganised remains of the adhesive base. C ($\times 9$).—Regular tufted growth of a *Scytonema*; upright branches arise from a basal tangle, the former then branch abundantly, the ramifications being arranged to form a fairly regular palisade-like layer. D ($\times 12$).—Dense tufted growth of *Schizothrix*, arising from an adhesive base.

cases this incrustation is due to carbonate of lime, but in other cases it is not affected by acids, and it has as yet been impossible to determine its exact nature. It seems plausible to associate this incrustation with the presence of the air, and possibly the latter may be a result of the formation of the former. The phenomenon is certainly no casual one,* as it is to be met with quite frequently in different parts of the island; the species exhibiting it are in part common forms throughout the lowlands, and are by no means always found with the associated air.

The third type of growth is the "tufted" one,† and is characteristic not only of many of the Cyanophyceæ, but also of the species of *Trentepohlia*.‡ In each tuft the filaments are firmly intertwined with one another to form bundles (fig. 1), which stand out approximately vertically from the substratum. The free ends of the filaments thus project outwards, and are occasionally considerably elongated and practically unbranched (frequently in *Scytonema* and *Tolypothrix*); sometimes the projecting ends are of a different (generally brighter) hue than the remaining parts of the filaments. The tufts are often (notably in *Schizothrix*, fig. 1, D) so closely placed that, if they all happen to be of the same length, it is difficult without the aid of a lens to determine the composite character of the growth; on the other hand, in the genus *Symploca* the tufts are generally quite isolated from one another. Where a rich tufted growth occurs, the substratum presents a velvety appearance owing to the numerous vertical tufts of intertwined filaments, and this pilose covering is like a wet sponge in the rainy season. The least pressure squeezes water out of it. The tufted type of growth constitutes the prevalent habit in *Symploca, Schizothrix* (fig. 1, D), etc., and a number of forms which assume the tangled type of growth at first, subsequently raise their filaments into tufts; such are *Tolypothrix, Scytonema* (fig. 1, C), *Stigonema*, etc., especially the species of the first-named genus varying very much in their manner of growth.

* In a few cases, encrusting unicellular forms were found to exhibit the same characteristic association with a film of air, although not growing in protected situations; the forms involved are species of *Glœothece*. Here also the thick outer lamellæ of the sheaths in most of the colonies were provided with a thin incrustation of a substance whose nature I have been unable to determine. Under the microscope, one or more air-bubbles are seen to be associated with each colony, being frequently drawn out into a kind of beak, the apex of which is in very close connection with the sheath of the Alga.

† I must point out that the terms "tangled," "tufted," etc., refer to the macroscopic appearance of the Alga. Under the microscope, many Algæ of the adhesive type show a tangle of filaments and, in the tufted form of growth, the filaments in each tuft are entangled with one another to a varying extent.

‡ Some of the species of *Trentepohlia* exhibit a slight tangled growth at first, while the basal disc ("sole") is, of course, always adhesive.

These forms, and especially those exhibiting pure tufted growth (*i.e.*, in which there is little or no tangled base), readily absorb moisture from the substratum by capillary attraction, whilst as long as the air is relatively dry (as compared with the substratum), water will also be given off by evaporation from the outer ends of the tufts, so that a constant circulation of water will take place. On the other hand, when tufted growth occurs on a substratum which does not furnish much moisture, the outer ends of the tufts will carry on the reverse process, and absorb water-vapour directly from the air, provided the latter is sufficiently moist. The tufted type of growth is thus liable to be successful on all kinds of substrata provided the air contains the necessary amount of moisture. These suggestions as to the biological value of tufted growth seem to agree with the main facts of the distribution of the latter. We should expect not to find tufted growth or to see it restricted to well-protected situations in dry localities, in which both air and substratum furnish little moisture; and this is really the case, for at Anuradhapoora, Negombo, etc., such subaërial growth as does occur is almost exclusively adhesive or tangled.* On the other hand, the wetter the locality the more abundant does this type of growth become; even at Kew it only occurs in the very damp hothouses (*e.g.*, the *Nepenthes*-house).

Atmospheric moisture thus seems to be the chief factor determining the development of tufts, and there is good reason to look upon them as being the result of a hydrotropic stimulus (*cf.* also below). The subaërial Cyanophyceæ under discussion, although they have left the aquatic habitat, are still semi-aquatic in their requirements, and it is not surprising to find moisture influencing them in various ways (*i.e.*, general distribution and mode of growth). In moist localities (*i.e.*, where there is plenty of water-vapour in the air) the advantage of the tufted as compared with the tangled type of growth is obvious, especially in exposed situations where the surface layers of the soil are very liable to be dried up by the heat of the sun's rays, so that absorption of atmospheric moisture is imperative. In damp localities, probably, all tangled growth sooner or later passes over into a tufted one or becomes colonised by some other species with tufted growth, but in dry localities the latter affords too ready a means of evaporation and, consequently, is unfavourable. Without experimental study the conditions of respiration in this form of growth can hardly be compared with those in a tangle; in all probability, however, they are much the same in the two cases.

Some of the species of *Trentepohlia* quite conform to the above-described method of growth (*e.g.*, *T. abietina*, Hansg.), whilst others differ in the great

* These observations were, of course, made during the dry season; possibly during the wet period tufted growth may be more commonly developed at these localities.

elongation of the filaments, which hang down in long tresses (*e.g.*, *T. arborum* (Ag.) De Willd.).

The last type of growth presented by the subaërial Cyanophyceæ is really only a modification of the tufted one; it may be spoken of as "stratified." It is found in the same species as exhibit the tufted habit, although on the whole it is of rare occurrence—a result, probably, of the absence of the special conditions which lead to its development. It was mainly observed in species of *Tolypothrix* and *Scytonema*. The characteristic feature of this type of growth lies in the fact that the closely-placed tufts are arranged in regular strata forming tiers one above the other; each tier generally projects a little beyond the one above it, and in this way a habit recalling that of some species of *Hypnum** or one of Schimper's "Etagenbäume" is attained. Such growth is mainly to be found on vertical walls or tree-trunks, where the species of Alga concerned often formed huge coherent sheets, which with some little trouble could be detached in their entirety. Since this type of growth occurs mainly in shaded situations, it may be suggested that the projection of each tier beyond the one above it enables the free growing ends of the tufts to obtain the maximum amount of light; in some cases these free ends were differently coloured to the main inner mass, and these differences in coloration may be a result of the illumination (see p. 206). It seems possible, therefore, that "stratified" growth is the result of tufted growth on a vertical surface in a shaded situation, and that stratification meets the requirements of illumination combined with the largest possible extent of surface-development. But moisture may also play some part in determining this type of growth, for, if one tier of tufts is once established, others might gradually grow out below and elongate sufficiently to catch up the drops of rain running off from the tier above; in this way tier upon tier might be formed. In this connection two points may be noted: Firstly, the tufts of a tier in their entirety point downwards, so that superfluous rain-water readily runs off one tier on to the next; and, secondly, "stratified" growth occurs on substrata which probably do not furnish much water in themselves. Both illumination and moisture may thus be concerned in the development of the stratified mode of growth, but I am inclined to regard the former as more important.

A few words may be added on the localities in which these different types of growth seem to predominate, and on their inter-relation. In exposed situations in the wet regions it is usual to find only one or other of the last three types of growth (mainly the tufted one), so that ordinarily only such

* *E.g.*, *Hypnum* (*Hylocomium*) *splendens*. *Cf.* Goebel, 'Organographie d. Pflanzen, Jena, 1898—1901, p. 56, fig. 27. Such growth is, of course, of quite a different nature to the case we are considering, but there is a considerable superficial resemblance.

substrata are colonised as are suitable for their development. Tree trunks and smooth rock-surfaces, even in very wet localities, are often only provided with a very poor algal covering, since the hard bark or rock is suitable only for adhesive growth; the latter, however, probably meets with considerable obstacles in the way of establishing itself owing to the very heavy downpours of rain which scour the surface of the tree or rock. If these difficulties are successfully overcome in early stages, adhesive growth may become established, and will then, in course of time, prepare the way for other forms of growth. Decayed trunks, of course, form a much more suitable substratum and generally bear rich algal growth of various kinds. In protected situations adhesive growth becomes well developed, especially on walls, rocks, embankments, etc., and is almost invariably the forerunner of tangled and tufted growth. In many cases it is quite possible to detect the remains of an adhesive growth at the base of tangled or tufted growth (fig. 1, B, D); mostly, however, such adhesive growth is quite dead. It appears more commonly to consist of unicellular encrusting forms than of filamentous species, and the former by their decay probably afford a kind of soil for further colonisation. In the dry regions, adhesive growth is predominant everywhere. Heavy downpours of rain probably make it impossible for larger gelatinous forms to obtain a foothold except in very sheltered situations. Tangled growth, since it helps to bind the clay of an embankment together, and to make it more suited to withstand a heavy downpour of rain, is liable on such a substratum to be much more successful in exposed situations than an adhesive growth; and such embankments may furnish a foothold for tangled forms without any previous growth taking place, although in many cases there is a passing preliminary growth of the adhesive type. The tangles again give way to tufted growth, which generally gains the upper hand ultimately. This tufted growth, as already mentioned above, may belong to the same form as constitutes the basal tangle, or may be due to a distinct tufted species. Thus *Symploca* is very commonly found growing on a basal tangle of *Tolypothrix*, whilst in other places small Mosses are found arising vertically from a similar base or even from a dense tufted growth of one species or the other. In both cases I frequently found some of the filaments of the basal tangle of *Tolypothrix* using the *Symploca* or the Moss, as the case might be, as a kind of support round which they twined themselves closely (fig. 2); they thus raise their filaments out into the air and, in fact, form a kind of upright growth quite comparable to a tuft,* at

* This, no doubt, also illustrates the mode of formation of a tuft. One or two outstanding branches first arise from a tangle, and these serve as supports for further branches which grow up round about them.

FIG. 2 (×72).—Tufted Growth of *Tolypothrix*, colonised by Bryophytes. The Alga is using the latter as a support by means of which it raises its filaments up into the air. The free ends of these filaments are appearing at all points. Only the sheaths of the individual filaments are shown.

the expense of the *Symploca* or Moss. Such cases very clearly illustrate the tendency of the filaments of a tangle to grow away at right angles to the substratum, and the stimulus is here undoubtedly a hydrotropic one. The ultimate effect of Moss, etc., being used as a support by the Alga on which it first settles down will be to more or less kill the former, and it can only save itself by growing out more and more as it gets entwined and killed off behind. In this way a thick layer of humus will gradually accumulate and serve as a base for the development of higher plants (small ferns, etc.). This is probably the way (after preliminary adhesive and tangled growth) in which bare rock-surfaces become gradually converted into substrata suitable for all kinds of growth. The subaërial Cyanophyceæ play a great part in the progressive colonisation of bare surfaces in the tropics, and to their agency the wealth of vegetation on every conceivable object is primarily due.*

* This subject will receive fuller treatment elsewhere (see "The *Rôle* of Algal Growth in the Colonisation of New Ground, etc.," in a forthcoming number of the 'Geographical Journal'); *cf.* also Treub, 'Ann. Jard. bot. Buitenzorg,' vol. 7, 1888, p. 213.

(ii) *The Upland Vegetation.*—The following description is based on an examination of the subaërial algal vegetation at Nuwara Eliya and neighbourhood. Although only six days (in the early part of the rainy period) were spent in this region, they were adequate for obtaining a general conception of the character of the subaërial Algæ, and I do not consider it likely that other parts of the uplands will differ very materially. Nuwara Eliya lies at a height of 6200 feet above the sea, and close at hand is Pedrotallagalla, the highest point of the island (8296 feet). The rainfall is a fairly high one (91 inches at Hakgalla) and, consequently, the subaërial Algæ are well developed, nearly every rock, tree-trunk or embankment being covered with them. This algal growth, however, bears a very different stamp to that of the moist lowlands, whilst Bryophytes and Lichens obtain a foothold, and even attain an abundant development in situations which are dominated by the blue-green Algæ in the low country. In all shaded localities, indeed, the greater part of the algal growth becomes completely obscured by Mosses and Lichens; it is best developed on smooth rock-surfaces or smooth clay-embankments in more or less exposed situations, which are apparently not so favourable for the growth of the other plants mentioned. A point which very soon strikes one with regard to the subaërial Algæ of the uplands is the great scarcity of the tufted mode of growth, so characteristic of the wet lower regions. The majority of the Algæ altogether exhibit the adhesive type, and by far the most of them are of highly gelatinous consistency. I have put together the following table with the object of showing the relative frequency of the four types of growth in the lowlands, in the country round about Peradeniya and in the uplands; the percentages are calculated from the actual number of cases examined:—*

Type of growth.	Lowlands.	Peradeniya.	Uplands.
	Per cent.	Per cent.	Per cent.
1. Adhesive	25	47·5	66·5
2. Tangled	34	35·0	26·5
3. Tufted	34 } 41	17·5	7·0
4. Stratified	7 }	—	—
No. of cases examined	56	40	30

The great prevalence of the adhesive habit is very manifest, and such tufted growth as occurs rarely covers any great extent of surface; tangles

* The species of *Trentepohlia*, which always assume a tufted habit, are not taken into account in the calculation of the above table; their tufts are probably not dependent on exactly the same conditions as the short dense tufts of the Cyanophyceæ, for they are just as common in the uplands as in the low country.

are rather more frequent. Embankments are generally covered with a thin slippery film of gelatinous forms (*e.g.*, the whole embankment along one side of Lady Horton's walk at Nuwara Eliya), and only at a few points are these overgrown by tangles or tufts. The Algæ (*Nostoc, Aphanocapsa, Glœocapsa, etc.*) concerned in the formation of these gelatinous films are all characterised by having very highly mucilaginous (almost diffluent) sheaths. But it is amidst the thick growth of Mosses and Lichens on the trunks of trees that these gelatinous Algæ often attain their greatest development; both on the wooded slopes of Pedrotallagalla and in the jungle on the Hakgalla rock the luxuriance of their development is remarkable. In most cases the Mosses are the more important epiphytes, but here and there gelatinous Algæ vie with them, either covering whole portions of the trunk like the exuded resin or latex of an injured tree or hanging down in long, jelly-like masses between the Mosses and Lichens.* Such growth would be almost an impossibility on a bare trunk, whilst it easily obtains a foothold and maintains its position amongst the growth of Mosses, etc. The rocks occurring in these jungles are remarkably poor in algal growth, which is probably due to the absence of forms with a type of growth suited to such a substratum. An almost diffluent *Nostoc* is not well suited for attachment to a smooth rock-surface in a rainy region, and such growth as does occur on these rocks is tangled† or very rarely tufted. The preceding remarks indicate one of the chief factors in the uplands, viz., the competition of the Bryophytes, etc.; bearing this in mind, we can understand the scarcity of tufted and tangled growth on moss-covered substrata, for it must inevitably become overgrown sooner or later by the prolific Bryophyte and Lichen vegetation.

There are thus very obvious differences between the subaërial Algæ of the lowlands and those of the uplands, but the exact factors leading to this diversity are difficult to determine. As above indicated (p. 207, footnote), gelatinous forms with semi-liquid, diffluent sheaths, do not get on successfully in the lowlands, because they are probably too susceptible to desiccation. In the part of the uplands studied, the relative humidity of the air is considerably greater than in the lowlands, whilst the temperature is, of course, lower, and these seem to be the chief factors determining the enormous

* The most important of these gelatinous forms are species of *Glœocapsa*, *Glœothece*, *Aphanocapsa*, *Nostoc*, and *Stigonema*. *Glœocapsa sanguinea* (Ag.), Kütz, possessing characteristic red-coloured sheaths, was particularly common on some of the tree-trunks at higher altitudes.

† In one or two cases I met with tangles associated with a film of air such as were described for the lowlands on p. 208. They are, however, of rather rarer occurrence in the uplands.

development of gelatinous forms in these regions—in many localities to the practical exclusion of other types of growth. But competition, encouraging the growth of the more successful gelatinous forms, cannot always be the explanation of the absence of tangled or tufted growth; such competition can scarcely play a part on an embankment. Here it seems as though the highly mucilaginous substratum afforded by the prevailing gelatinous adhesive growth is not a suitable base for growth of a higher type. A more complete analysis of the prevailing conditions will probably cast more light on the matter.

The subaërial algal flora of the uplands of Ceylon has a certain superficial resemblance to that of a damp region in the temperate zone, but it differs in its luxuriant development and in the important part played by the blue-green element. The light-conditions in particular, but also the temperature during the day (at least at most times of the year) are distinctly tropical—witness the wealth of the Phanerogamic vegetation. The green algal element, which is of considerable importance in the subaërial vegetation of our parts, is still quite crowded out by the more successful blue-green forms; their success is here again probably, to a large extent, due to adequate protection from the strong illumination. It should be noted, however, that I met with terrestrial species of *Vaucheria* (*V. sessilis* (Vauch.) DC.) at one or two points round about Nuwara Eliya—forms which, as far as my observations go, are entirely wanting in the lowlands.

The subaërial algal vegetation at places like Kandy (rainfall, 82 inches) and Peradeniya is approximately intermediate in its character between that of the lowlands and uplands, although on the whole savouring more of the former (*cf.* table on p. 215). In the wet regions of the lowlands we have a profuse subaërial flora, which is probably in the main due to the high temperature, whilst in the true uplands the rich algal growth is the result of a rather high rainfall. At Peradeniya and neighbourhood both factors are not so strongly developed, the temperature being low compared with that of the low country, and the rainfall less than at Nuwara Eliya and neighbourhood. In correspondence with this we find a marked decrease in the extent of development of subaërial algal vegetation at Peradeniya and in the surrounding country. In the wet jungles on the hillsides round Peradeniya, however (*e.g.*, at Hantane), we meet with a state of affairs rather like that on Pedrotallagalla, although on a less luxuriant scale. Otherwise the subaërial algal vegetation in these regions stands behind both that of the lowlands and uplands, and cannot even compare, for instance, with that at a place like Matara (rainfall only 69 inches !). The character of the algal vegetation is of particular interest. Tufted and tangled growths are fairly well repre-

sented (*cf.* table on p. 215)—especially the latter, which is no doubt a result of the relative dryness of the atmosphere. Gelatinous adhesive forms are much commoner than in the lowlands, although rarely exhibiting that markedly diffluent character which is such a feature in the uplands; the species of *Nostoc*, for instance, occurring round about Peradeniya, are more of the foliose type with a fairly consistent investment. The arches of the aqueduct in the experiment station at Gangarruwa, probably owing to the abundance of moisture, are exceptional, since at most points they are densely overgrown by a highly gelatinous *Nostoc* in all hues of brown and green to almost colourless.

A few words on the subaërial Algæ found on the cliffs and rocks of the sea-coast may be added, based on observations made at Matara, Ambalangodda, Bentotta, and Trincomalie. In all cases the substratum is probably subjected to occasional spray from the sea (in stormy weather), but otherwise the conditions are identical with those influencing the lowland subaërial Algæ generally. Cyanophyceæ are the prevalent forms, and especially in the higher zones their character is quite similar to that presented by the inland forms above discussed. The lower parts of the cliffs and occasional rocks on the sea-shore, on the other hand, tend to be colonised by a characteristic assemblage of unicellular blue-green forms (species of *Placoma*, *Radaisia*, *Entophysalis*, and *Chroothece*), which are more or less marine in character; their habitat is, no doubt, much more often reached by the sea-water, and this factor excludes the ordinary inland algal growth to a varying extent, whilst it calls forth the marine element just mentioned. The subaërial algal growth on the sea-coast finds an interesting parallel in the algal vegetation of fresh-water pools, which are found in the sand of the sea-shore at diverse points, and will be considered in Part II of this paper; in both cases the occasional advent of sea-water brings in a modifying factor.

(b) *Algal Vegetation of the Inland Fresh-waters.*

In this section I propose to deal with the macrophytic algal vegetation (both attached and floating) of the numerous pieces of inland fresh-water (excluding rivers) I had the opportunity of studying. Since the essential conditions influencing the character of the algal vegetation in these pieces of water are much the same in all cases, I shall deal with them in detail in the following discussion of the tanks, and merely point out the differences, when speaking of the other pieces of fresh-water. Minor factors cause the variation in the flora noticeable in the different collections of water.

(i) *Algæ of the Tanks and other Large Inland Masses of Fresh-water.*—The tanks are pieces of fresh-water of artificial origin, and often of very

ancient date; they occur all over the island, but are especially common in the dry northern half. They have partly been made by the damming up of broad river valleys, and partly by the collection of rain-water in specially prepared hollows. In a few cases they occupy natural hollows in some of the large basaltic masses which occur at many points (*e.g.*, Nalande and Dambulla). Large numbers of small shallow tanks are found near every village in the drier parts of the island. Tanks of medium size, and apparently of some depth, are Madawachyawewa,* Kekunadurewewa, Villamkulam,* Habaranewewa, Periyakulam, Kurunegalawewa, and we may also include here the lakes at Kandy, Colombo, and Nuwara Eliya. A few of the tanks are of very large dimensions; of these I was able to examine the following (approximately in order of size, beginning with the largest): Lake Mineri, Kelawewa and Balaluwewa, Nuwarawewa, Tissawewa, Basawakkulam, Lake Kantelai, the last named being shallow throughout.†

The algal flora is well developed in most of the tanks, and, as far as the present state of affairs is concerned, their conditions of life are practically natural. The special conditions may be briefly considered first. The illumination is, of course, very intense, for the tanks are, as a rule, exposed to the full glare of the sunlight.‡ Trees and bushes only rarely come down to the water's edge, and the immediate neighbourhood of the bank tends to be inhabited either by dead trees, whose bleached trunks and branches look like spectres in the distance, or, at the best, only by a stunted growth, owing to the frequent changes of water-level. The edges of the tanks on the water-side are generally occupied by a rich growth of water-weeds

* The termination *wewa* is the Singhalese name for tank, *kulam* is the Tamil designation.

† It is almost impossible to obtain a boat on any of the tanks, and the presence of crocodiles generally makes wading impossible. On the whole, therefore, my observations are confined to the vegetation within a few feet of the water's edge. It would have been interesting to examine a few of the smaller tanks a little more completely, but the littoral region is, after all, generally the most abundantly populated, and most likely to afford important results from our point of view. In all cases I made a point of walking round more than half the embankment of each tank, so as to obtain a good general idea of the type of growth it contained. I was able to investigate Lakes Mineri (by the courtesy of Mr. McPhail) and Kantelai more completely with the help of a boat, and also the lakes at Colombo (by the kindness of the Colombo Rowing Club), and Kandy (by the courtesy of Mr. Baird).

‡ Oltmanns has recently pointed out ('Morph. u. Biol. d. Algen,' vol. 2, 1905, p. 190), that an important consideration with regard to the conditions of illumination influencing aquatic algal growth is the quantity of light which gets reflected at the surface of the water. Not only is the intensity of the light much greater in the tropics, but, owing to the more or less vertical position of the sun, a far smaller percentage of the light is reflected at the surface. I was only rarely inconvenienced by the glare of light from the surface of the tanks (*cf.* also Ewart, in 'Annals of Botany,' vol. 12, 1898, p. 379).

(*Myriophyllum indicum*, *Trapa bispinosa*, *Nymphæas*, *Neptunia oleracea*, *Aponogeton monostachyon*, *Limnophytum obtusifolium*, *Chara*, etc.), and beneath these numerous algal forms generally find shelter. In some tanks the muddiness of the water, in others an abundant Plankton (notably *Clathrocystis !*) serve as a screen to the remaining life in the water. As a general rule (which is, however, by no means without exceptions, *cf.* table on p. 224), a tank with a poor Plankton is not rich in any kind of algal growth (*e.g.*, Kurunegalawewa, Nalandewewa), whilst one with a fairly abundant Plankton generally contains a good deal of other algal vegetation (*e.g.*, Kelawewa, Lakes Mineri and Kantelai). On the other hand, it seems that, in some cases, the Plankton may become so extremely abundant that it does not allow of the passage of sufficient light for any other noticeable growth; this was the case in the tanks at Dambulla (*Clathrocystis !*) and Habarane (*Clathrocystis* and *Pediastrum !*). The Plankton is, of course, in no way the only source of shading in the tanks, and where there is a well-marked growth of water-weeds, for example, these may shelter abundant Algæ, although the Plankton is poor.* The light to which the aquatic Algæ of the tropics are subjected, however, always remains very strong, and it is, therefore, not surprising to find the Cyanophyceæ again predominating (probably owing to their protective pigment, *cf.* p. 206), although, perhaps, not to such a marked extent as in the subaërial vegetation

We have already, in the preceding section, learnt to associate the Cyanophyceous element with a high temperature, and this is, of course, the second condition to which the flora of tropical waters is subjected. Leaving the lakes at Kandy and Nuwara Eliya out of consideration, the approximate mean daily temperature of the water near the edge of the tanks is 28°·5 C.; the lowest temperature observed (6 a.m.) was 25° C., which is only attained on hot summer days in our parts; the highest temperatures (from 10 a.m. to 2 p.m.) range from 30° to 35° C.,† the latter in shallow tanks like most of the smaller ones, as well as Kantelai and Sigiri; in the deeper tanks (*e.g.*, Villamkulam, Dambulla tank) the temperature does not seem to rise much above 30° C. In the shallow tanks the range of daily temperature is very considerable (viz., from 25° to 34°·5 C. in Lake Kantelai, for example) and, in the small tanks, such a wide range is probably the rule. Even in the deeper tanks the range is apparently

* Attention may be drawn to the fact that in the absence of water-weeds, the green macrophytic algal growth of the tanks is almost invariably attached; floating green patches only occur in those tanks in which the abundant growth of large aquatics furnishes a considerable shelter against the strong light.

† The temperature of a warm bath is about 35° C.

considerable, and not far behind that of the air (*e.g.*, in Villamkulam, water from 25° to 30° C.; air from 24° to 30°·5 C. in the shade) at least, as far as the surface-layers of the water are concerned. These observations, which, of course, refer to the temperature round the margins of the tanks only, and apply also to all the different kinds of inland fresh-waters, show that a very high temperature is frequently attained during the day, and that there is a considerable, though gradual, cooling over night, which, however, never results in a temperature which would be considered anything but warm in our parts. It seems probable from what is known that a considerable number of fresh-water Algæ prefer rather cold water,* and this may be one of the causes of the practical absence of a number of green forms from the fresh-waters of the tropics (*cf.* below). On the other hand, most of the Cyanophyceæ seem to flourish best in warm waters, and hence their preponderance in the aquatic flora of Ceylon. The relatively high temperature of tropical waters, however, also involves the solution of a proportionally smaller amount of oxygen and carbon dioxide. Especially the smaller percentage of oxygen, and the consequent greater difficulty of respiration, seems likely to be an important feature, although it remains to determine its influence by exact experiment. I incline to asume that this is one of the chief causes of the practical absence of certain temperate genera from the waters of the tropics, and that it also accounts for certain peculiarities of tropical fresh-water algal growth.†

The temperatures of the upland waters are, of course, in no way so high; thus lake at Kandy (10.30 a.m.) = 25° C.; lake at Nuwara Eliya (8 a.m.) = 16° C., the latter being almost temperate, although on hot sunny days the water probably becomes rather warmer than it ever does in our parts. The range of daily temperature is certain to be very considerable here (*cf.* introduction).

The third condition to which the algal vegetation of the tanks is subjected is a frequent change of water-level, which probably takes place with a rapidity unknown in our parts. During the dry period some of the smaller tanks decrease to more than half their normal size, and are then surrounded by very poor meadow-land with stunted grassy growth, the external portions of which are often occupied by the dead trees above referred to; the limit of the tank in the wet season is well marked by the fringe of dense jungle, which begins some

* *Cf.* Oltmanns, *loc. cit.*, vol. 2, 1905, pp. 186 and 187.

† *Cf.* Warming, 'Ökologische Pflanzengeographie,' Germ. Ed., Berlin, 1896, p. 121. "Dass das Absorptionsvermögen des Wassers für Gase mit steigender Temperatur abnimmt, ist vielleicht der wesentlichste Grund, weshalb gewisse Wasserpflanzen im Sommer . . . verschwinden"; *cf.* also *loc. cit.*, p. 124.

little way behind high-water mark. Towards the end of the dry season even the larger shallow tanks are very much reduced, being surrounded by large areas of meadow-land, marshy in character near the water but dry and bleached beyond. In the deeper tanks (*e.g.*, Mineri, Nuwarawewa) the sinking of the water is not so noticeable, although the bleached algal remains on the exposed stonework of the dams bear testimony to the height of the water in the wet season. The rise of the water-level can take place very rapidly, and the change produced by a single night's heavy rain is remarkable.* As soon as the rains commence the shallower tanks are surrounded by a wide stretch of shallow water devoid of any algal growth; this latter will, of course, put in an appearance subsequently, but the few tanks that I was compelled to examine in the (beginning of the rainy) season gave quite barren results in this respect. That an abundant growth of Algæ and other water-weeds does often take place in the later portion of the rainy period is evidenced by the decaying remains left behind on the sinking of the water-level in the dry season. Where the irrigation-works are in working order they tend to prevent the water-level from rising above a certain height.

More important than the actual variation in the height of the water-level are the consequent sudden changes in the concentration of the matter dissolved in the water; this cannot be without effect on a group so delicately constituted as that of the fresh-water Algæ, and possibly this is a cause for the poor development of the algal flora in some of the tanks.

Whereas the three preceding conditions (light, temperature, and change of water-level) are practically the same in every piece of lowland fresh-water (especially the last two), we have now to consider those factors which differ from tank to tank and are in all probability frequently the cause of the minor variations in the algal flora; these are: chemical composition of the dissolved matter in the water, degree of movement in the water, nature of the substratum, and muddiness of the water. These (together with the conditions of illumination) are just the same features as are probably the main cause of the variation in the algal flora of temperate waters, but in the tropics the dominant conditions (light, temperature) are the determining factors for the general character of the fresh-water flora and, consequently, the minor conditions have a rather different basis to work upon. My time was too limited to enable me to collect many data regarding these minor factors and

* According to Mr. McPhail, the local engineer, the water-level in the huge expanse of Lake Mineri may rise as much as 10 feet in the course of one night. This tank is supplied by a number of mountain streams, which, when the rainy season commences, pour large masses of water into it. At Lake Kantelai I observed a rise of several inches in the course of a single night.

their bearing upon algal vegetation in the waters of Ceylon, but I saw enough to satisfy myself that a careful study would probably reveal somewhat analogous algal associations in the tropics to those occurring in our parts of the world.

I will now briefly consider the minor factors, and will begin with the little I can say regarding the chemical composition of the water. Some of the tanks must certainly be rich in dissolved organic substance owing to the large amounts of water-weeds they contain;* in other cases the fæces of the abundant water-fowl must contribute to the organic contents. The frequent presence of Characeæ probably means dissolved carbonate of lime.

Most of the smaller tanks are sheltered from the ordinary winds, and the water, even at the edge, was usually quite undisturbed at the time of my visit. In the larger tanks, on the other hand, a relatively large surface is exposed to the wind, so that there are usually numerous small waves at the edge; the littoral flora is therefore growing in water, which is frequently disturbed and well aerated (especially noticeable in Nuwarawewa, Tissawewa, and Lake Mineri).

The substratum in the tanks is muddy or clayey except where the tank occupies an excavation in the rock (*cf.* p. 219). In Balaluwewa and Villamkulam part of the substratum seems to be sandy. The dams are often mere clay embankments, but in a number of the larger tanks are made up of blocks of rock, and these rocks, of course, afford a suitable base for lithophytes when under water.

In many of the smaller tanks the suspended particles of mud are of an exceedingly finely divided nature, giving the water a yellow colouration; these particles are so fine that they often take several days to settle completely. The water of these tanks (*e.g.*, Punchikekirawa, Mancadawawewa) is generally, but not always (*e.g.*, tank between milestones 101 and 102 on road from Vavoniya to Madawachya), poor in organic life, and this latter consists mainly of animals.

Briefly summarised, the conditions of life of the macrophytic Algæ in the Ceylon tanks are thus as follows:—Strong illumination; high temperature of considerable daily range (varying from 6° to 10° C.); small amount of

* Thus, especially in Tank Basawakkulam and Lake Kantelai, the edge was fringed by an accumulation of partly bleached and partly putrid remains of *Chara*, *Myriophyllum*, etc., many yards in extent, and I have little doubt that such a mass of decomposing water-weeds forms the bottom of the entire lake. Round about the edge of Lake Mineri I also found *Chara* washed up in large amount. It is a well-known fact that especially Cyanophyceæ prosper very well in a medium containing dissolved organic substance (*cf.* p. 227, and also Kirchner, in Engler u. Prantl, 'Die Natürl. Pflanzenfam.,' I Teil., Abt. 1*a*, 1900, p. 63).

dissolved oxygen in the water; periodic (often rapid) change of water-level, causing exposure for the attached forms of the higher zones and change in concentration of the water for the forms of the lower zones; mostly a muddy or clayey substratum with occasional rocks (detached from the dams); water which is generally almost stagnant.

Looking upon the algal flora of the tanks in its entirety (we may even for a moment include the Plankton in these remarks), one is struck by the fact that in a considerable number of them it is completely dominated by the blue-green element.* The table below may serve as an illustration of this point; the various tanks studied are classified in three series according to the composition of Benthos and Plankton. Those tanks of the first series which are provided with an asterisk contain practically nothing but Cyanophyceæ; the remainder have a noticeable green element, although still entirely dominated by the blue-green. It also seems of interest to notice the relative amounts of Phanerogamic vegetation present;

Table to show Essential Composition of Algal Growth in Ceylon Tanks.

<table>
<tr><td>Littoral growth, blue-green.
Plankton, blue-green.</td><td>Plankton only, blue-green.
Littoral growth, green.</td><td>Plankton, green.
Littoral growth, green.</td></tr>
<tr><td rowspan="3">**Colombo Lake** (!).
Kandy Lake (!).
Nuwarawewa.
Interconnected:
Tissawewa (!).
Basawakkulam.
***Tank in Anuradhapoora Gardens.**
***Town tanks, Anuradhapoora.**
Madokotaikulam (near Vavoniya).
Madawachyawewa.
***Dambullawewa** (!) (Plankton only!).
*Neravieawewa (!).
Habaranewewa (!) (Plankton only!).
Tank at Sigiri.
***Pokuna on top of rock Sigiri** (!) (Plankton only!).
Lake Mineri.
***Lake Kantelai.**
***Andankulam.**
Hiriwadunnawewa (near Habarane).</td><td>**Villamkulam.**
Tirappanewewa.†
Balaluwewa.
Periyakulam (near Trincomalie).</td><td rowspan="3">Pond in Peradeniya Gardens.
Interconnected:
Kelawewa.‡
Mancadawewa† (animals common).
Punchikekirawa.‡
Ekiniyeawewa.†
Malawewewa.†
Balankulam‡ (near Anuradhapoora).
Madakanawewa.‡
Mahakadawellawewa.
Namoluwewa.
Megaswewa (!)† (Plankton only!).
Wendrenkulam† (Plankton only!).
Kurunegalawewa (Plankton only!).
Senadiniyagawawewa (!) (near Habarane) (Plankton only!).
Borlasgamawewa.‡
Tibbotuwawewewa.
Koilpuliumkulam (near Vavoniya).
Malawewewa.‡</td></tr>
<tr><td>Littoral growth only, blue-green.
Plankton, green.</td></tr>
<tr><td>Nalandewewa (!)†.
Walikulam (near Kekirawa).
Karambawewewa.
Yaka-anaguhuwewa (near Habarane).
Mahakekirawa.
Kekunadurewewa (!)†.</td></tr>
</table>

* I, of course, exclude the green Phanerogamic vegetation, which is often abundantly developed in tanks which are otherwise completely dominated by the blue-green forms.

† Plant life very poorly represented.

‡ With a noticeable admixture of blue-green forms.

where this latter is poorly developed, an exclamation mark in brackets is added.

At first sight this table may not appear to bear out the above statement of the dominance of the blue-green element very clearly, but a consultation of the map will show that all the large and important tanks and lakes come into the first or second columns, the only noticeable exceptions being Kelawewa and Kurunegalawewa.* I may also point out that of the tanks enumerated in the third column, five (all near Kekirawa) are probably in connection with one another and with the waters of Kelawewa, and that a considerable number of them (five) are very poor in organic life altogether, which cannot be said of any of those in the first column. I have endeavoured to bring out this latter point more clearly by employing heavy type for those tanks which have an abundant algal vegetation (either littoral or pelagic or both). It will be seen that whereas nearly all the tanks with a dominant blue-green vegetation are rich in Algæ, this is only the case with respect to two of the tanks in the third column. In further illustration of this point, I append lists of tanks in which the green and blue-green forms respectively are negligible (the same arrangement of type is preserved):—

Green Element negligible.	*Blue-green Element negligible.*
Basawakkulam.	Mancadawawewa.
Tank in Anuradhapoora Gardens.	Punchikekirawa.
Town Tanks, Anuradhapoora.	Tibbotuwawewewa.
Dambullawewa (Plankton only !).	Malawewa.
Madawachyawewa.	Senadiniyagawawewa (Plankton only !).
Neravieawewa.	Namoluwewa.
Pokuna on top of Sigiri (Plankton only !).	Megaswewa (Plankton only !).
Lake Kantelai.	Wendrenkulam (Plankton only !).
Andankulam.	Kurunegalawewa.
Hiriwadunnawewa.	Borlasgamawewa.
	Mahakadawellawewa.

As an outcome of these considerations, we may state that whenever there is a well-developed algal flora in the considerable number of Ceylon tanks and lakes I have examined there is *always a noticeable blue-green element which very frequently dominates the entire algal growth.* If we now attempt a comparison of the features just discussed with those of other tropical

* It is an interesting point that the dominance of the blue-green element is most pronounced in the larger tanks. The smaller tanks probably present conditions somewhat analogous to those prevailing in the smaller pools and ditches (viz., greater risk of sudden desiccation, and stagnant water with less aeration ; *cf.* the next section of this chapter). The smaller tanks thus gradually carry us over to the small pieces of water considered subsequently.

regions, we meet with serious difficulties, for our existing tropical algal floras, though doubtless of considerable systematic and phytogeographical value, are practically useless from this point of view. I have nowhere found a particular comment on the dominance of the blue-green element, although Messrs. West and West* remark on the presence of well-developed individuals of *Clathrocystis* in tropical Plankton. However, I do not hesitate to suggest that in other parts of the tropics the blue-green element plays the same important part that it does in Ceylon, in some cases to a less, in others, perhaps, even to a more marked extent, according as the external conditions vary. I shall return to this subject elsewhere,† and need here only point out that in view of the very distinct aspect of the fresh-water algal vegetation in the tropics it is certainly astonishing that its general character has not previously been subjected to a critical analysis.

I will now endeavour to give a brief sketch of the essential character of the blue-green macrophytic Algæ (excl. Plankton), and of their mode of occurrence in the different tanks of Ceylon.‡ The blue-green vegetation forms either (*a*) a dense felt or tufted growth or adhesive film on submerged rocks, tree-stumps, etc.; or (*b*) floating masses, the latter in particular often attaining a very prominent development. The more important and characteristic floating forms belong to the genera *Oscillaria*, *Lyngbya*, *Tolypothrix*, *Scytonema*, *Hapalosiphon*, and *Rivularia*. A member of the second genus (*L. majuscula* (Dillw.) Harv.) is exceedingly common in many of the tanks (*e.g.*, Nalandewewa, Tissawewa, Balankulam, Madawachyawewa, Habaranewewa, etc.), forming large dark-green floating masses of densely interwoven coarse filaments. At Nalande and Anuradhapoora it completely dominates the vegetation of all the waters fed by the respective tanks; at the latter place many of the smaller tanks threaten to become completely silted up by the growth of this Alga and by the mud which collects amid the tangle of its filaments. Other (smaller) species of *Lyngbya* also occur in the tanks (*e.g.*, in Villamkulam, Andankulam), but play no very important part (see, however, the next page).

Another very important constituent of the algal vegetation of the tanks are species of *Rivularia* (*Glœotrichia*). They absolutely dominate the algal flora in Basawakkulam (*Glœotrichia Rabenhorstii*, Bornet), and also play a great part

* West and West, "Observations on the Conjugatæ," 'Annals of Botany,' vol. 12, No. LXV, 1898, p. 36.

† 'Annals of Botany,' April, 1907, p. 243 *et seq.*

‡ When the water of the tanks falls in the dry season, a number of pools are usually left behind, which, of course, again constitute a part of the tank in the wet season. The vegetation of these pools is taken into account as a constituent part of that of the tank in the following remarks, wherever it is deemed necessary.

in Lake Kantelai (*Glœotrichia natans* (Hedw.), Rabenh.). These two tanks, it is interesting to notice, are both characterised by a very rich growth of water-weeds, so that their waters certainly contain a very considerable percentage of organic substance (*cf.* above, p. 223, footnote); further, they are both practically stagnant. Whether these factors are directly related to the abundant occurrence of *Rivularia* in these tanks must for the present remain an open question. Whereas in Basawakkulam the *Glœotrichia* is the only common Alga, this cannot be said of Lake Kantelai, where another blue-green form (*Lyngbya œrugineo-cœrulea* (Kütz), Gom.) is exceedingly common, and shares the dominance of the former. The *Lyngbya* (like the *Glœotrichia*) is attached to the segments of the abundant water-weeds, covering them with its thin flocculent films for considerable stretches: in places this growth is so profuse that it forms thick yellowish-green masses immediately below the surface of the water. Exactly the same species occurs in abundance attached to the submerged aquatics (*Myriophyllum* and *Chara*) in the open waters of Lake Mineri (together with small quantities of *Glœotrichia*), but here it forms very delicate films, tending to break up on being touched. In both Mineri and Kantelai, however, the films do not consist of pure *Lyngbya*, but give shelter to a considerable number of unicellular forms (various blue-green species; Diatoms, notably *Epithemia* and *Pinnularia;* Desmids, *e.g.*, species of *Cosmarium*), the whole constituting a very characteristic assemblage of algal species. The Diatoms and Desmids occurring in these films are in part quite identical for the two tanks, and the films are thus a good example of the "consortia" discussed below.* It is only open to surmise as to whether there is anything more than a kind of "space-parasitism" in the case of these composite films,† but there seem possibilities of more important (nutritive ?) interrelations which we are not yet in a position to understand.

Oscillaria, though rarely of great importance in the floating flora of the tanks, was a prominent feature in Mahakekirawa; here *O. tenuis*, Agardh. var. *natans* (Kütz), Gom. occurred as small floating discs (2 to 6 inches in diameter, and often almost perfectly round) on the surface of the water. The filaments are arranged in a radiate manner in these discs, which also include a considerable quantity of yellowish mud, serving to increase their compactness. No doubt the discs originate on the mud at the bottom of the tank, and

* See p. 247 and *cf.* Fritsch, "Problems in Aquatic Biology," etc., 'New Phytologist,' vol. 5, 1906, p. 157.

† Inasmuch as Lakes Mineri and Kantelai are the only large tanks I have had the opportunity of studying from a boat, I consider it very probable that such *Lyngbya*-films may occur in the open water of a number of the other tanks, especially as the films are not at all commonly found near the banks, but attain their greatest development over the deeper portions of the tank.

are ultimately raised to the surface by gas-bubble development (*cf.* below, p. 240). Similar discs are sometimes to be observed in temperate regions, but their development has, as far as I am aware, not been studied.

Scytonema (*S. tolypotrichoides,* Kütz) was a dominant form in only two of the tanks, viz., Madokotaikulam near Vavoniya and Karambewawewa, near Anuradhapoora. In both cases it formed spherical ægagropilous masses floating round the margin and consisting of large quantities of knotted, more or less radially arranged filaments, frequently of a yellowish colour on the surface, although deep blue-green in the interior of the spherical structure. The tangle of filaments, no doubt, includes air, by virtue of which the masses, which are often about double the size of a cherry, float. The mode of development of these masses has not been studied, but is probably analogous to that of the ægagropilous *Cladophoras,** depending on successive movement of the growing structure into various positions by the currents in the water.

There is much greater specific diversity to be found in the attached Cyanophyceous growth than among the floating forms, which, as the above remarks will have shown, are referable to a small number of species; the most important attached forms belong to the genera *Oscillaria, Lyngbya,* and *Tolypothrix.* In comparison to our parts, the practical absence of unicellular species in the attached blue-green flora is noteworthy. The dense pilose tufted growth found on submerged rocks (especially Lake Kantelai), tree-stumps, etc., is usually not due to a single species, but is composite (both blue-green and green with intermingled Diatoms, viz., *Synedra, Navicula, Surirella*). There is probably no essential difference between the attached growth in the majority of the tanks, and that found in many of the small pools (*cf.* below); in both cases we are dealing with algal consortia.†

We will now turn our attention to the composition of the green algal element in the flora of the tanks. It exhibits a number of characteristic features (common in part to the algal flora of all the inland waters), which are, on the whole, just as striking as the dominance of the Cyanophyceæ, viz.:—

(*a*) The practical absence or great scarcity of certain genera, such as *Cladophora, Rhizoclonium, Vaucheria, Ulothrix,* and *Conferva,* and the consequent scarcity of a number of epiphytic Diatoms so characteristic of the fresh-water algal flora of our parts (*e.g., Cocconeis Placentula, Synedra splendens*).

(*b*) The replacement of *Cladophora* by the genus *Pithophora.*

* *Cf.* especially Brand, "Die *Cladophora*-Ægagropilen des Süsswassers," 'Hedwigia,' vol. 41, 1902, p. 34 *et seq.;* and Wesenberg-Lund, "Sur les *Ægagropila Sauteri* du lac de Sorö," 'Bull. Ac. R. d. Sci. et d. Lettres Danemark,' 1903, No. 2, p. 167 *et seq.*

† A few further facts regarding the attached growth on rock-surfaces in the tanks are mentioned in the section dealing with the algal flora of the rock-pools (p. 248).

(*c*) The important part played by the genus *Spirogyra* to the practical exclusion of other filamentous Conjugates, and the special systematic composition of this *Spirogyra*-element.

(*d*) The usually marked absence of broad filamentous forms (excepting *Spirogyra*).

The genus *Cladophora* and its ally *Rhizoclonium* are exceedingly rare in Ceylon,* and the explanation of their absence seems no very difficult one. In our parts they generally frequent water which is well aerated, and in larger pieces of water, for instance, are in great part confined to near the banks, where there is plenty of motion owing to the wind.† The practical absence of these two genera in the fresh-waters of Ceylon is probably due to an insufficiency of dissolved oxygen. The thick coarse walls and broad filaments of these genera are not well suited for a ready diffusion of gases. The absence of *Vaucheria* also may be due to its broad filaments, although (as far as the tanks are concerned) this genus is not a very common constituent of lake-vegetation, even in our parts. *Vaucheria,* however, has a decidedly different assimilatory process to that of most other green Algæ, and it is possible that this process does not go on readily amid tropical conditions. This view may receive some measure of support in the fact that the entire group of the Heterokontæ (Confervales, Borzi), which probably have a similar assimilatory process,‡ is very rare in the lowlands of Ceylon.§ Ulotrichaceæ are certainly also§ rare in Ceylon, and their scarcity is not easy to understand. Some species of *Ulothrix* are known to favour aerated water (although this does not apply to all of them), and possibly the small percentage of dissolved oxygen may have something to do with their absence. We have practically no data regarding the influence of the amount of dissolved oxygen on the different genera of Algæ, but it seems very likely that some of them may be far more susceptible

* The following remarks (to last paragraph on p. 231) apply to the fresh-waters of the Ceylon lowlands as a whole.

† *Cf.* Chodat, "Algues vertes de la Suisse," 'Pleurococcoïdes—Chroolépoïdes,' Berne, 1902, p. 77; also p. 90.

‡ Regarding this assimilatory process, see especially K. Bohlin, "Studier öfver några slägten af Alggruppen Confervales, Borzi," 'Bih. K. Svenska Vet.-Ak. Handl.," vol. 23, Afd. III, No. 23, German Résumé, pp. 52—54. The chloroplasts contain a relatively large amount of xanthophyll, and the first product of assimilation appears to be a glucose, which subsequently becomes transformed into oil. The assimilation is thus decidedly different to that of the remaining green Algæ, and in the conditions of illumination, temperature, etc., prevalent in the tropics, there may be some factor or factors unfavourable to the process of photosynthesis in this case.

§ Messrs. West and West ("Fresh-water Algæ of Ceylon," 'Linn. Soc. Trans.,' vol. 6, 1902, p. 124) have already commented on this subject.

in this respect than we imagine, so that tropical conditions may even exclude forms which favour stagnant water in our parts.

We will now briefly notice the occurrence of representatives of the groups and genera just discussed in Ceylon waters. I have practically only met with fresh-water species of *Cladophora* in two wells (at Matale and Ambalangodda, see p. 250), *i.e.*, in well aerated water. *Rhizoclonium*, a genus which is exceedingly common in our temperate waters, was scarcely met with except in the estuaries and lagoons. On the other hand, the most important representative of the Cladophoraceæ in Ceylon is quite undoubtedly the genus *Pithophora*, which, although neither a very common form, was met with sufficiently frequently to make it a sensible constituent of the algal flora. It was never found in the actual tanks except in those of small size, but generally occurred in the side-pools above mentioned (p. 226, footnote). The species of *Pithophora* have, on the whole, thinner cell walls* than either *Cladophora* or *Rhizoclonium*, so that they may be in a better position to withstand the increased difficulty of respiration in the tropics. *Pithophora* may, however, in its spores also have a far better adaptation to the vicissitudes of the tropics (desiccation) than either of the two other genera;† this is a point which should not be very difficult to settle experimentally. If we examine into the existing records of the occurrence of species of *Cladophora* and *Rhizoclonium* in the tropics, we find that in most cases (where the habitat is at all adequately described!) these forms were growing in flowing or otherwise well aerated water.‡ The remaining cases do not prove anything to the contrary until it has been definitely ascertained that the water in which these forms were growing was actually stagnant. I think it may be safely stated that both *Cladophora* and *Rhizoclonium* are rare forms in tropical fresh-waters, and that they normally only appear in a well aerated habitat. They are replaced by the genus *Pithophora*, which apparently flourishes quite well in stagnant waters.

I have met with *no species* of the genus *Vaucheria* in the lowlands of Ceylon (terrestrial and aquatic species in the uplands! *cf.* pp. 217, 254),

* See especially Wittrock, "On the Development and Systematic Arrangement of the Pithophoraceæ," 'Nov. Act. Reg. Soc. Sc. Upsala,' Ser. 3, 1877, p. 8: "The vegetative cells . . . . have all a thin membrane of cellulose without layers. In Cladophoreæ, particularly the cells belonging to the lower part of the thallus have often a thick membrane in distinct layers." See also the plates illustrating the paper cited.

† It is interesting in this connection to mention that Miss F. Rich, working jointly with me on the biology and ecology of British fresh-water algal growth, has come to the conclusion that *Cladophora* deserts those ponds which are subject to drying up in summer.

‡ The records of tropical Algæ found in the existing literature will be considered more fully elsewhere ('Annals of Botany,' vol. 21, No. LXXXII, April, 1907, p. 248 *et seq.*).

although one may regard my collections as fairly representative of the algal flora. A consideration of the published papers further brings out the startling fact that very few determinable fresh-water species of this genus have been recorded from the tropics, and there are only few records of terrestrial species (chiefly *V. sessilis* (Vauch.), DC.).* In the course of my travels I came across many likely localities for the occurrence of *Botrydium*, but I never found it; there are only three records from the tropics (from Loanda in Africa, Brazil, and Ecuador). We may, therefore, further characterise the algal flora of the tropics by the practical *absence of fresh-water species of Vaucheria*, and the extreme scarcity of the terrestrial Siphoneæ (*Vaucheria* and *Botrydium*).

I must here refer to another feature which is intimately connected with the rarity of *Cladophora*, *Rhizoclonium*, and *Vaucheria*, viz., the scarcity and different composition of the epiphytic growth, which in our waters finds one of its main substrata on the filaments of these genera. The characteristic epiphytic Diatoms (*Cocconeis*, species of *Gomphonema*, *Synedra splendens*, etc.) are very rare in the Ceylon fresh-waters, which may, in part, be the result of the lack of a suitable substratum. But even where I found *Pithophora* with a well-marked epiphytic growth, it was not made up of the above-mentioned species of Diatoms, but usually consisted largely of species of *Achnanthes*.

The entire group of the Confervales seems to be poorly represented in the tropics; only three genera (*Characiopsis*, *Conferva*, and *Ophiocytium*) have been recorded and, except in the case of *Ophiocytium*, the records are rather few in number.† In Ceylon I have only met with occasional filaments of *Conferva* in fresh-water, although future more detailed examination of my material may disclose small numbers of the unicellular forms. Whether the peculiar type of assimilation in this group is really responsible for its scarcity in the tropics can only be settled by a careful investigation of those tropical localities in which members of this group appear.

The Conjugates are amongst the most important constituents of the green element in the algal flora of the tanks, and it will be best to consider the Conjugate vegetation of these latter separately from that of the other pieces of Ceylon fresh-water. The Conjugates are best developed in those tanks which possess a rich growth of water-weeds; where larger aquatics are wanting, conditions are not favourable for the growth of any floating green Alga, which is bound to rise to the surface during the hot hours of the day, and so be fully exposed to the strong sunlight. The development of the filamentous Conjugate element in the tanks takes place almost entirely at the expense of species of *Spirogyra; Mougeotia* is exceedingly rare (*M. parvula*, Hass.,

* *Cf.* 'Annals of Botany,' *loc. cit.*, p. 254. † *Loc. cit.*, pp. 256, 257.

var. *angusta*, Hass. in Tissawewa), whilst I never met with a *Zygnema* in any of the tanks. Looking at the species of *Spirogyra* found in the Ceylon fresh-waters in their entirety, it is very noticeable that they all belong to the section in which the transverse walls between the cells are simple and not infolded, and that the large majority have more than one or even two spiral chromatophores in each cell. These features are, in the main, common to all the *Spirogyras* of tropical waters, although they do not appear to have been noted before. Of 38 species recorded from the tropics, only nine* have cells containing a single chloroplast, and only five have infolded transverse walls. Infolding of the end-walls of the cells is commonly met with in many of the narrower *Spirogyras* of our waters, and is generally regarded† as a mechanism for the dissociation of the cells of the filament, but its exact function is not perfectly understood, nor do we know why it occurs in one species and not in another. Since the large majority of tropical *Spirogyras* are broad forms, and infolded walls are only found in the narrower species, we could in no case expect to find many examples of the latter type; yet the interesting fact remains that the few narrow forms nearly all have simple end-walls. It is just as difficult to account for the prevalence of broad forms with numerous closely-arranged chloroplasts in each cell. Except for the species of *Pithophora*, the *Spirogyras* are the only Algæ with broad filaments found at all commonly in the tropics, all the remaining forms being narrow and rarely exceeding 15 μ in diameter. I am inclined to associate this with the fact that *Spirogyra* gets on well in stagnant water under relatively unfavourable conditions of respiration (perhaps owing to the thin cell-wall), so that forms with broad filaments are as successful as the narrow ones (*cf.* next paragraph and also p. 221). I am unable to offer any explanation for the usual abundance of chloroplasts.

The most important forms in the attached green algal flora are species of *Œdogonium*.‡ Floating masses of this genus are rather rare (only in Madokotaikulam and Madakanawewa), although this may be a seasonal phenomenon. The species of *Œdogonium* found in the waters of Ceylon are, as a rule, narrow forms with filaments having a diameter of 9—12 μ, even 15 μ being rather rare; species with broad filaments are exceptionally

* Sixty-two records of *Spirogyras*, with a number of chloroplasts, as compared with 20 records of forms with a single chloroplast. The details will be given elsewhere (Fritsch, in 'Annals of Botany,' vol. 21, No. LXXXII, April, 1907, p. 260 *et seq.*).

† *Cf.* Oltmanns, *loc. cit.*, vol. 1, 1904, pp. 57, 58. On the whole, my material shows very few cases of breaking up of the filaments into their constituent cells, though the conditions must frequently have been favourable for dissociation. This is probably due to the absence of those species of *Spirogyra* (viz., those with infolded end-walls), which most commonly exhibit this phenomena.

‡ The genus *Bulbochæte* is of rare occurrence in the tanks, and was always only observed in small quantity amongst other attached Algæ.

rare. The numerous records of species of *Œdogonium* from the tropics show a very considerable preponderance of narrow forms.* As already pointed out above, the filamentous algal flora of the tropics is prevalently narrow, *Spirogyra* and *Pithophora* being the only broad forms at all commonly met with. This is no doubt due to the smaller percentage of dissolved oxygen in the water, forms with narrow filaments being better suited to these conditions than broader ones. The phenomenon finds its parallel in the extensive subdivision of the foliage in many of the higher aquatics. *Spirogyra* and *Pithophora* are probably able to exist as broader forms, owing to their thin cell-walls admitting of more rapid diffusion of gases. A careful study of the tropical habitats of broad species of *Œdogonium* will probably disclose some special factor favouring their development. Possibly the rather limited occurrence of *Pithophora* may also be due to the necessity of some special condition. The *Spirogyras*, however, are too widely distributed to admit of such an assumption.

The Chætophoraceæ do not constitute a very important element, but species of *Stigeoclonium* were observed in some amount in a few cases (*e.g.*, Balaluwewa, Habaranewewa), whilst *Aphanochæte* is occasionally found as an epiphyte on other filamentous Algæ. *Chætophora* was not seen in the tanks. *Coleochæte* is an occasional epiphyte.

The lake at Nuwara Eliya, the only large piece of upland water studied, could, unfortunately, only be subjected to a very cursory examination. There is no doubt, however, that the flora is in no way dominated by the blue-green element. At the time of my visit there was very little algal growth.

(ii) *Algæ of Roadside Ditches and Pools in the Lowlands* (excluding rock-pools, see Section iv).—Although the tanks are the most important pieces of inland fresh-water in Ceylon, a considerable bulk of algal growth is also found in the numerous small pools and roadside drains occurring all over the island. The general character of this vegetation is in most respects similar to that of the tanks, but there are certain noteworthy differences which require a brief discussion. The above-mentioned pools (p. 226, footnote) which are found round about the tanks in the dry season, but constitute part of them when the water rises, occupy an intermediate position between isolated pools and the actual tanks as far as their algal flora is concerned. They generally, however, approach more nearly to the latter, since their flora is (to a great extent at least) dependent on that of the tanks, and is consequently dominated by rather different conditions than apply to the pools, etc., which form the chief subject of discussion in the present section. Most of the forms found in the pools around the tanks are also met with in the main waters of the

* *Cf.* Fritsch, 'Annals of Botany,' April, 1907, p. 265 *et seq.*

latter, but from what I have seen I think it probable that certain species are able to flourish better in small isolated pieces of water than in the large expanse of the waters of the tanks, and consequently attain to a degree of development in these pools during the dry season, which is impossible except in such small collections of water. Further, algal spores carried by the wind or other means of dispersal may produce an algal growth in the side-pools, which would never be successful in the main tank.

The conditions to which the Algæ of the pools and ditches are exposed are the same as those above defined for the tanks, although most of them are more emphasised.* Thus, except where shading is afforded by the surrounding trees and bushes, the shallow character of these pieces of water means little or no protection from the strong light, and in the absence of shade algal growth is rarely found. The temperatures attained are very high, and there is a very considerable daily range. The risk of desiccation is great, and drying up or inundation can take place very rapidly. The water is in almost all cases quite stagnant, heavy downpours of rain being the only source of aeration. The conditions of life are on the whole more uniform than in the tanks, the most essential variations lying in the degree of shading and the frequency of desiccation, conditions which are to some extent mutually dependent.

In the pieces of water under consideration the blue-green element, although still well developed, does not play the same predominant part as in the tanks. The Conjugates are here the dominant group, almost every pool or ditch examined containing a certain and often very considerable amount of *Spirogyra*,† whilst other Conjugate genera (especially *Zygnema*, more rarely *Mougeotia*) are of frequent occurrence, though rarely present in great quantity. The dominance of *Spirogyra* is very noticeable on comparing the vegetation of these pieces of water with that of the segregated pools round about the tanks, for in the latter *Spirogyra* only occupies the second place, as in the actual waters of the tanks. It is not easy to understand why the Conjugates play so important a part in the pools and ditches, whilst the Cyanophyceæ are subsidiary to them. It seems very probable that it is not so much the occurrence of special factors which favours the Conjugate element, but rather the existence of one or more conditions unsuitable to the blue-green element, so that it becomes weakly developed and gives room for the *Spirogyra*, etc.

* Some of the smaller shallow tanks come very near to the pieces of water under consideration (*cf.* footnote on p. 225).

† The species of *Spirogyra* in the pools and ditches show the same general features as those of the tanks (viz., simple end-walls and a prevalence of broad forms with many spirals in each cell).

Thus the *Spirogyras* may be better suited to meet the emergencies of desiccation than most of the aquatic Cyanophyceæ (which generally have a rather poorly developed sheath as compared with the subaërial forms) owing to the ease with which they form resting spores. Azygospore-formation is not uncommon in my material, and although we are quite ignorant as to the rapidity with which such azygospores are formed, it seems reasonable to conclude that it is a much more rapid process than the sexual development of zygospores. In case of approaching desiccation, which in the tropics will often take place very rapidly, there will be a sudden concentration of the water, and this may well act as a check on ordinary conjugation and lead to the formation of azygospores.* The prevalence of *Spirogyra* may, however, also be due to the frequent strong shading† of these pieces of water, or to the success of *Spirogyra* in perfectly stagnant waters such as these, both conditions which though, perhaps, not unfavourable to the blue-green element, may still enable the Conjugates to flourish and crowd out the Cyanophyceæ. In comparison with pools and ditches in temperate regions, however, the blue-green Algæ still play a relatively important part, whilst Conjugates are much more strikingly abundant. Without there being much difference in generic constitution the facies is quite another one.

In a number of the pools and ditches examined, *Spirogyra* was practically the only form present, but in other cases it is accompanied by a subsidiary vegetation composed of *Œdogonium*, *Microspora*, *Zygnema*, *Mougeotia*, *Bulbochæte*, *Ulothrix*, *Stigeoclonium*, and various Cyanophyceæ‡ (*Anabæna*, *Lyngbya*, *Oscillaria*, *Scytonema*, etc.); in a few cases one or other of these forms (nearly always *Œdogonium*) was dominant, while the *Spirogyra* takes a second place.

* *Cf.* Klebs, 'Die Bedingungen der Fortpflanzung bei einigen Algen und Pilzen,' Jena, 1896, p. 246 *et seq.* In *Spirogyra Weberi* a 4-per-cent. solution of cane-sugar induced the formation of a large number of azygospores, whereas in *S. inflata* a 6-per-cent. solution was necessary to interfere with ordinary conjugation and produce parthenogenesis; in this latter species a 4-per-cent. solution induces ordinary conjugation, so that a sudden increase in concentration from 4 to 6 per cent. leads to parthenogenesis.

† Messrs. West and West ("Observations on the Conjugatæ," 'Annals of Botany, vol. 12, No. XLV, 1898, pp. 35, 36) point out that the Conjugates can stand prolonged exposure to fairly strong light in their natural habitat, which is not quite in agreement with the statement that the effect of such exposure is to induce the formation of zygospores (*cf.* also Ewart, "The Action of Cold and of Sunlight upon Aquatic Plants," 'Annals of Botany,' vol. 12, 1898, p. 379 *et seq.*). It would seem as though strong light stimulated the reproductive functions which probably means cessation of the vegetative activities. On the other hand, Conjugates appear to be rather less sensitive to illumination than many of the other filamentous green genera, and it is possible that the tropical members of this order are adapted to a fairly strong light.

‡ Except for occasional floating forms, the Cyanophyceæ occur most commonly attached to water-weeds and branches and twigs lying loosely in the water.

It is interesting that if the latter genus is entirely wanting Cyanophyceæ generally take the lead (*cf.* the remarks in the preceding paragraph). Desmids are occasionally very abundant, whilst other unicellular and colonial green forms (Protococcales, etc.) are rare in these lowland waters; colonial Cyanophyceæ (*e.g.*, *Merismopedia*, *Gomphosphæria*) are sometimes not uncommon. In comparison with temperate regions the scarcity of Diatoms is very noticeable, which is not difficult of explanation when one recollects that these forms have a preference for cold water, and even in our parts generally attain their maximum during the winter months. Yet both Diatoms and Desmids are a good deal commoner in the pools and ditches than in the tanks.

The large majority of these pools and ditches of the lowlands are characterised by a *Spirogyra-Œdogonium** vegetation, the latter genus, though relatively rarely attaining abundant development, being almost invariably present in some quantity. This vegetation acquires different aspects according to the subsidiary forms present and is particularly well emphasised in certain pools and ditches owing to the almost constant association of other species with the *Spirogyra* and *Œdogonium*.

The pools and ditches thus characterised always exhibit a dense, brownish-red granular deposit on the bottom, and the same deposit often also constitutes a filmy investment to all the water-plants. This deposit consists of ferric hydroxide, and I will consequently talk of these pieces of water as ferruginous pools.† Such pools are very common in all the lowland regions with a considerable rainfall (*e.g.*, Negombo, Colombo, Hanwella, etc.), and are not rare in the uplands around Nuwara Eliya. Owing to the uniform character of the algal flora, these ferruginous pools may all be considered together (*i.e.*, both those of the lowlands and uplands). In a dozen typical cases examined from different parts of the island, neither *Spirogyra* nor *Œdogonium* were ever found to be absent from the pools, although the one or the other (very rarely both) was occasionally only present in small quantity. Of other filamentous forms, various species of *Bulbochæte* (including *B. minuta*, West and West, *B. spirogranulata*, West and West, etc.) are rarely wanting, and may be regarded as a constituent of almost equal importance to the two genera previously mentioned; they invariably occur as epiphytes on larger water-weeds, and possibly their absence in some few cases is the result of the lack of a suitable substratum. *Ulothrix*,

* The species of *Œdogonium* found in these pieces of water are again prevalently narrow (see p. 232).

† Similar deposits are also found in the rice-fields, and these waters show the same characteristic flora as that now to be described.

Microspora, and *Zygnema* are all casual forms in these pools, these being the only habitats in which species of *Ulothrix* occur at all commonly in the island. Of much greater importance for the characterisation of the ferruginous pools are certain Desmids (fig. 3) and Diatoms. Foremost among

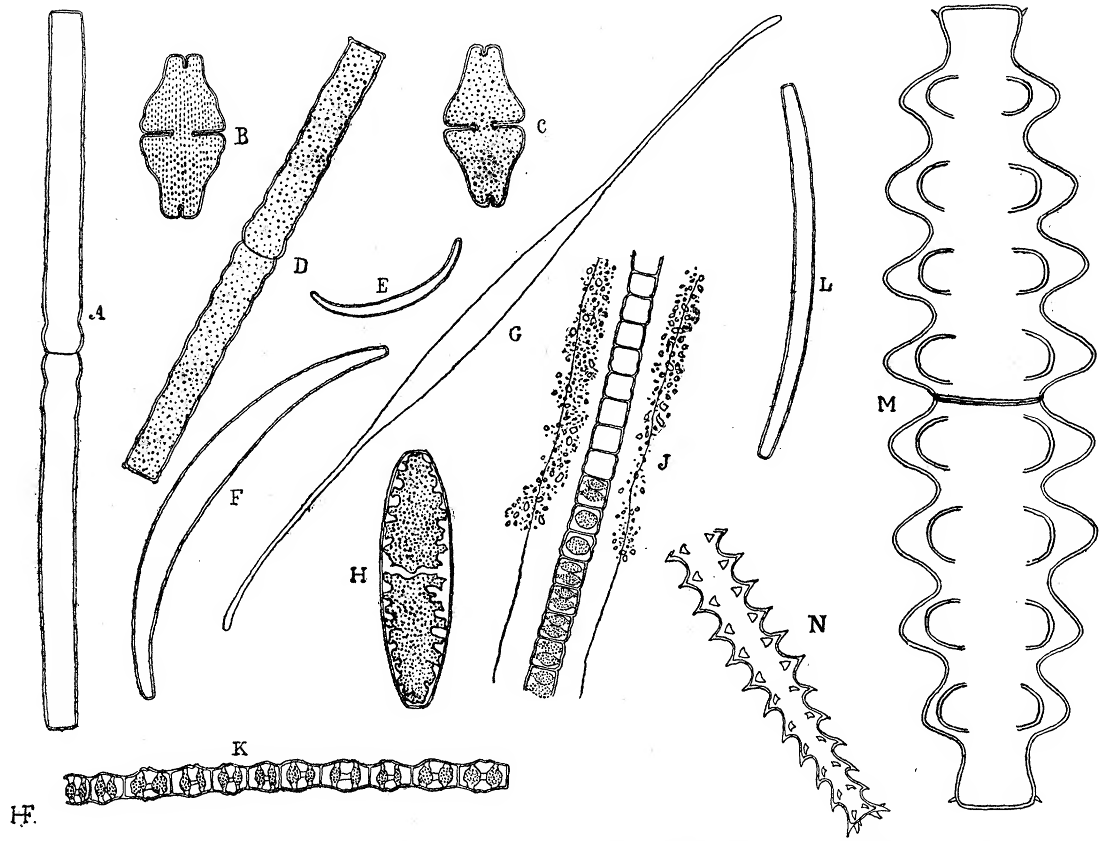


FIG. 3.—A few of the more Characteristic and Typical Desmids of the Ferruginous Pools (all magnified about 260 diameters). A, *Pleurotænium Trabecula* (Ehrenb.), Näg. B, *Euastrum ansatum,* Ralfs. C, *Euastrum obesum,* Joshua f. *punctatum.* D, *Pleurotænium annulatum,* West and West. E, *Closterium Venus,* Kütz forma. F, *C. pseudodianæ,* Roy. G, *C. setaceum,* Ehrenb. H, *Netrium digitus* (Ehrenb.), Itzigs. and Rothe. J, *Hyalotheca dissiliens,* Bréb. K, *Gymnozyga moniliformis,* Ehrenb. L, *Closterium abruptum,* West. M, *Pleurotænium nodosum,* Lund. N, *Triploceras gracile,* Bail.

the Desmids are species of *Pleurotænium* (*P. Trabecula* (Ehrenb.), Näg.; *P. annulatum,* West and West; *P. trochiscum,* West and West; *P. nodosum,* Lund.; *P. doliforme,* West and West, etc.); diverse forms of *Triploceras gracile,* Bail.; species of *Closterium* (*C. setaceum,* Ehrenb.; *C. abruptum,* West; *C. Pseudodianæ,* Roy; *C. Venus,* Kütz, etc.; in the uplands, also:

C. Leibleinii, Kütz, and *C. Jenneri*, Ralfs); species of *Euastrum* (*E. ansatum*, Ralfs; *E. obesum*, Joshua; *E. dideltoides*, West and West); and *Netrium digitus* (Ehrenb.), Itzigs. and Rothe; *Cosmarium*, *Penium*, *Staurastrum* (more frequent in the uplands!) and *Spirotœnia* are of minor importance and often scarcely represented. A number of filamentous Desmids* (*Gymnozyga moniliformis*, Ehrenb.; *Hyalotheca dissiliens*, Bréb.; *Micrasterias foliacea*, Bail.;† and more rarely species of *Desmidium*) are also characteristic forms in these pools. Amongst the Diatoms, *Pinnularia* and various small species of *Navicula* play the most important part, although only of occasional occurrence. *Pleurosigma* and *Surirella* seem to be characteristic in some cases, whilst, where water-weeds are present, *Synedra lunaris*, Ehrenb., sometimes occurs as an epiphyte on them. The blue-green element is often entirely wanting in these pools, and is never of any importance.

Before proceeding to discuss the few data available regarding the biology of this flora, it will be well to briefly sum up its constitution as follows:—

(a) *Dominant.*—Species of *Œdogonium* and *Spirogya*, *Pleurotœnium Trabecula*, *P. annulatum*, *Closterium setaceum*, *C. pseudodianœ*, *Triploceras gracile*, *Netrium digitus*.

(b) *Subsidiary.*—Species of *Bulbochœte*, *Euastrum*, *Pleurotœnium*, *Closterium*, *Cosmarium*, *Pinnularia*, *Navicula*.

(c) *Occasional.*—The remaining forms mentioned above and a considerable number of others.

Of all the forms enumerated, only *Spirogya* and *Œdogonium* are absolutely constant, all the others being occasionally absent.‡ Their absence may be due to actual variations in this ferruginous flora, or to the pools examined being in diverse phases, the latter, on the face of it, seeming the more probable explanation. This brings us to consider the relation between the algal flora and the characteristic granular deposit found in these pieces of water. We are confronted by two possibilities. The flora may have nothing to do with the deposit, or the latter may be due to the activity of the Algæ present. Such evidence as I have been able to obtain points to the latter conclusion. Whenever there is a considerable growth of

* Filamentous Desmids are, however, only a marked feature of the lowland pools; they are rarely present in those of the uplands (*cf.* p. 253). There is a very marked filamentous tendency amongst these Desmids of the lowland pools; this is exemplified by the presence of a filamentous species of *Micrasterias*, a genus in which the individuals are usually single, and by the frequent occurrence of short filaments of *Triploceras gracile* and *Pleurotœnium* (*e.g.*, *P. annulatum*).

† This is the only species of *Micrasterias* I have as yet noticed in these pieces of water.

‡ *Pleurotœnium*, *Bulbochœte*, *Closterium setaceum*, *Triploceras*, and the species of *Navicula* are most widely present.

filamentous Algæ in these pools, large amounts of the granular deposit form a dense, reddish-brown flocculent investment all round the filaments (see, for example, fig. 3, J), so that the latter are often completely obscured; a similar coating is generally also found on any water-weeds present. It is hardly possible to account for this investment in any other way than by the assumption that it has originated round about the algal growth and water-weeds, as a result of their metabolic activities. The water of these pools contains a small amount of dissolved ferric chloride,* and this is probably transformed (oxydised) into an insoluble form by the vital activities of the plants present. As the ferric hydroxide accumulates, it sinks down to the bottom of the pool, and forms a granular layer there.† The gradual increase in the amount of the deposit may produce less favourable conditions (shading?) for certain algal forms, which thereupon disappear. In the diverse pools studied, many different cases suggestive of the above theory were met with. Thus, in some of the pools, the granular matter merely formed a flocculent covering to the contained vegetation, and there was little or none on the bottom; in others, there was a quantity of the reddish-brown deposit on the bottom, as well as enveloping the plant-growth present; whilst, in still others, there was only a dense granular layer on the bottom, and practically no vegetation rising up into the water above it. In the pools last mentioned the vegetation was generally scanty and least satisfactory, from the point of view of uniformity with the others. Such pools generally also contained a quantity of *Leptothrix*, and it seems as though this genus finds favourable conditions as the deposit accumulates; possibly it is the direct cause of the disappearance of the main mass of algal growth. In any case, the ultimate result of the accumulation of the red deposit is the elimination of a considerable mass of the vegetation. What this process leads to finally I am unable to say, but there are some indications of the initial state of affairs to be found in pools and ditches having no trace of the characteristic deposit, but containing a flora very similar to that above described.

* I have to thank Professor E. C. C. Baly, of University College, London, for kindly analysing this water.

† It is not impossible that iron-bacteria may have a hand in this process. They are well known to occur in such waters, and by their activity to give rise to extensive deposits of hydroxide of iron (*cf.* S. Winogradsky, "Üb. Eisenbacterien," 'Bot. Zeit.,' vol. 46, 1888, pp. 261—270). They would probably tend to collect about the surface of the members of the green vegetation, owing to the evolution of oxygen going on there; so that the red deposit would primarily appear round about the water-weeds and Algæ present. I do not, however, think that these deposits can be solely due to their agency, for in many cases there were very few bacteria evident; they seem to occur more commonly in later stages.

Although such ferruginous pools are very characteristic of Ceylon, they are not essentially tropical, and are found quite frequently in temperate regions. I have observed a similar reddish-brown deposit accumulating since several years in one of the small ditches on Sheen Common, Richmond (Surrey), and very much the same flora occurs associated with it as in the Ceylon pools. *Spirogyra, Œdogonium, Zygnema, Ulothrix, Conferva, Pleurotænium, Closterium, Netrium, Pinnularia, Navicula, Surirella,* and *Synedra lunaris* are the more important forms I have observed in the course of casual visits during the last three years. The species are apparently in many cases not identical with those found in the tropical pools, but that alters little in the astonishing similarity. During the period of observation, the granular deposit has steadily increased in quantity, while the Algæ have slightly decreased in numbers. Latterly, blue-green forms are putting in an appearance, which tallies with what I observed in Ceylon. The vegetation of these ferruginous pools thus constitutes one of the most striking cases of parallel between temperate and tropical algal formations that I have noticed, and probably stands isolated in this respect.

There is one more phenomenon noticed mainly in the pieces of water under discussion (also in the padi-fields), that may be briefly described. As above mentioned, pools without a noticeable Conjugate element are generally inhabited by Cyanophyceous growth,—often *Oscillaria.* A visit to such a pool in the early morning shows the muddy bottom covered with a more or less continuous film of the Alga, as is characteristic of the species of this genus. The film consists of a thin layer of algal filaments with a certain amount of mud between them. Soon after sunrise gas-bubbles make their appearance studded all over the surface of the films, whilst at many points the latter show signs of inflation indicating a similar development of gas-bubbles on the lower side. Soon after midday floating patches of *Oscillaria,* still with numerous adhering gas-bubbles, are found on the surface of the water, and a little patience enables one to follow the detachment and rising of such a patch to the surface. This state of affairs continues for the rest of the day, but early on the next morning there are again no floating patches of *Oscillaria,* which merely forms a film on the bottom. In the course of the day the same process repeats itself. This phenomenon is observed in waters which are shallow (and almost unshaded) and in which the midday temperature is very considerable (viz., 35° C.). The rise of patches of the films to the surface is, of course, due to the expansion of the gas-bubbles formed during the assimilation and respiration of the Alga, whilst the cooling of the water after nightfall involves a contraction and perhaps partial solution of these bubbles (and probably their consequent detachment), and this results in the sinking

of the floating patches. The phenomenon is certainly no rare one in the case of Algæ capable of forming compact discs like *Oscillaria* (*cf.* also p. 227). Analogous, though not absolutely similar, is the rising of tangles of filaments, occasionally also to be seen in *Oscillaria*, though more frequent in green filamentous genera such as Conjugates, *Œdogonium*, *Cladophora*, etc.* The facts mentioned in this paragraph are also, of course, commonly to be noticed in temperate regions, but I am not aware that a daily rise and fall of such constancy ever occurs in our parts.

It seems probable that the Algæ in this case are merely the passive objects of a useless physical phenomenon, and that the daily rise and fall is of no service to them. But it seems well to point out that the rising of the oscillariate patch to the surface may be advantageous from the point of view of respiration and of assimilation (the latter owing to the considerable percentage of mud included in these oscillariate films). In any case the Alga only avails itself of a physical process, which would take place whether it was of service to it or not.

(iii) *Algæ of Marshes and Padi-fields* (*i.e.*, of ground permanently or periodically saturated with water which does not form definite pools).—There is very little difference on the whole between the algal flora of the padi-fields and that of the lowland pools and ditches, but the biological conditions are a little different, and it is a desire to emphasise these that leads me to hold the two distinct. The rice-fields are fully exposed to the strong sunlight, and the only (very scanty) source of protection is the frequent muddiness of the water. Desiccation is a regular periodic phenomenon, and periodicity would probably be found to be better marked in this flora than in the algal vegetation of any other Ceylon fresh-water. In their exposed habitat the rice-fields resemble the tanks, whilst the desiccation risks are analogous to those in the small pools and ditches. In correspondence with this the blue-green element is rather more pronounced than in the latter, although the Conjugates still very often have matters their own way. The latter are sometimes almost the only forms present in a padi-field, but just as often there is practically nothing but Cyanophyceous growth. *Œdogonium* is not so commonly met with as in the pools and ditches, but *Bulbochæte* is again quite a common form. The Desmid-flora is often very rich, whilst in one or two cases Diatoms (*e.g.*, *Gomphonema* attached to water-weeds) were present in exceptional numbers. A very

* *Cf.* Oltmanns, 'Morphologie und Biologie der Algen,' vol. 2, Allgemeiner Teil, Jena, 1905, p. 142; also H. Devaux, "Du Mécanisme des Échanges gazeux chez les plantes aquatiques submergées," 'Ann. Sci. Nat. Bot.,' 7th ser., vol. 9, 1889, p. 144. In the case of filamentous green Algæ, etc., the bubbles are retained between the tangle of filaments and, by their alternate expansion and contraction, cause the rising and falling of the tangles.

characteristic member of the vegetation of the padi-fields is *Pleurosigma curvulum*, Pritch., though rarely present in any great quantity; another form frequently found in small numbers is *Fragilaria*. I did not meet with *Pithophora* or representatives of the Ulotrichales and Confervales in any of the padi-fields examined.*

The periodicity of the algal growth in the rice-fields would be an interesting study, and would probably disclose interesting adaptations, which a brief examination such as mine could not possibly reveal. It seems that the first growth is almost always blue-green, and that the green element only appears subsequently when the rice and occasional water-weeds (especially Characeæ) afford a certain amount of protection against the strong light. Two fresh rice-fields at Matale showed practically nothing but blue-green forms, whilst a slightly more advanced field at Matara contained abundant *Oscillaria* intermingled with occasional filaments of *Spirogyra* and Diatoms and Desmids in some numbers. Old rice-fields often contained only very scanty Cyanophyceæ, but in their place quite a rich Conjugate and Diatom flora. It almost seems as though after the harvesting of the rice, and with approaching desiccation the blue-green element again gains the upper hand, since dry padi-fields often bear a filmy growth of some blue-green form on the stiff mud. I think the sequence just sketched out is near the actual one, but there are certainly occasional exceptions.

I met with very few examples of marshy ground other than that afforded by the padi-fields. Mr. Lewis kindly pointed out a fairly typical marsh to me about two miles inland from Kalutara; the ground was saturated with water and covered by a rich growth of mosses with *Urticularia*, *Nepenthes*, etc. The algal flora was that characteristic of such habitats in temperate regions, viz., a very rich Conjugate flora with numerous diverse Desmids and a certain number of Diatoms. Blue-green forms on the whole played a minor part. A small extent of low-lying swampy ground about half-a-mile to the east of Matara was covered by a rich growth of grasses, and was in most respects unlike the marsh at Kalutara. The algal flora though rich in Zygnemaceæ was exceedingly poor in Desmids, and Diatoms were common only as epiphytes. There was a considerable growth of a narrow species of *Œdogonium* at some points.†

(iv) *Algal Vegetation of the Rock-pools.*—At diverse points (Nalande, Dambulla, Kurunegala, Habarane) in the northern half of Ceylon one meets

* It may once more be pointed out that the specific constitution of the green algal flora is exactly the same as in the pools, ditches, and tanks (*cf.* p. 228 *et seq*).

† One or two further (brackish) marshes will be considered in conjunction with the estuarine flora in the second part of this paper.

with huge black masses of basalt, which, besides forming the substratum of the local tanks, generally contain numerous small but deep pools, which often harbour an abundant growth of Algæ of a characteristic type, although the neighbouring tanks are generally very poor in littoral algal vegetation (often with a very rich Plankton, *e.g.*, Dambullawewa, Habaranewewa).* The temperature of the water in these pools is often high (31°·5 C. at Dambulla at 4 P.M.; 28°·5 C. at Hanwella at 8 A.M.; particularly high in the shallow pools at Kurunegala), but the daily range is certainly not very considerable, especially where the pools are deep, as at Dambulla and Nalande.† The pools are exposed to the full light, though the black rock-surface is probably a good absorber. The deeper pools, in particular, give one the impression of receiving relatively little light beyond the surface layers. The decided prevalence of Cyanophyceæ (especially in the shallower pools), however, speaks for the shading being less perfect than in the case of the pieces of water considered in Section (ii). The risk of desiccation is small in the deep pools, and it seemed as though many of the shallower ones owed their origin to springs. This would also mean good aeration, as is indicated by the whole aspect of the flora in many of the rock-pools; species characteristic of stagnant water are in most cases absent. The special conditions in these pools are thus: rocky substratum, high temperature of no considerable daily range (especially pronounced in the deeper pools), full exposure to light (except in case of deep pools), and probably fairly good aeration.

The algal vegetation in the rock-pools either takes the form of a close pilose or fluffy covering on the rocky sides, or of a floating mass. More than half the number (18) of typical pools examined contained a blue-green flora with very few other forms; this is what we should expect under the dominant conditions. The chief representatives of the Cyanophyceæ are attached species of *Rivularia* and *Hypheothrix* (see below) and floating forms

* Similar masses of basalt are found round about other tanks (*e.g.*, Punchikekirawa, and between Kelawewa and Balaluwewa), and are no doubt covered by their waters in the wet season, so that the pools in them then become part of the tank. During the dry period, however, the pools are isolated and show a certain amount of individuality, though strongly dominated by the flora of the tank. They are considered in the present section, however, owing to certain similarities to the true rock-pools, as also are some pools observed in rock-quarries at Hanwella. The characteristic rock-pools (*i.e.*, those which are not in connection with a tank) are distinguished in the above description as the "typical" ones.

† It should be pointed out that the water of these pools is not only heated directly by the rays of the sun, but indirectly through the medium of the surrounding rock. The latter will retain the heat much more tenaciously, and this will serve to decrease the daily range of temperature in the pools in the rock, especially in the deeper ones.

of *Anabœna* (sometimes also *Lyngbya,* mainly *L. majuscula*). Narrow species of *Oscillaria* are often present in minor numbers, but this genus plays a very unimportant part here in comparison to the pieces of water discussed in the previous sections. The absence of *Tolypothrix* is noteworthy. The blue-green element, though abundant, thus shows a very monotonous constitution, which is in striking contrast to the great diversity displayed by the green flora. This is very well developed in all the rock-pools not dominated by Cyanophyceæ, and also shows some uniformity in so far as it consists almost only of Conjugates and Protococcales. But, for the existence of forms belonging to these two groups, conditions must often be eminently suitable, for such pools have furnished a diversity of forms, which only finds its parallel in the upland pools. Diatoms (*Fragilaria, Navicula*) are rare—in fact often as good as absent (none in 11 of the pools), but Peridiniaceæ are often quite common amongst the members of the Conjugate vegetation. *Œdogonium,* if present at all, generally plays a very minor part amongst the Conjugates, although it attained considerable development in a pool at Kurunegala and one at Hanwella.* The species of this genus found in the rock-pools have generally rather broader filaments than the species inhabiting the waters previously discussed, although none of the forms could really be called broad. This feature may be connected with better aeration.

The abundant Conjugate element comprises certain species of Zygnemaceæ and Desmidiaceæ, and although these forms have been shown to play a part in the minor waters of the lowlands generally, we shall find that they exhibit a markedly different aspect in the rock-pools. In the first place *Spirogyra* is mostly only a subsidiary form, in many cases, indeed, of isolated occurrence; only in three of the 18 typical pools examined did it play an at all important part, whilst in nine of them it was completely absent (even in some cases in which the other Conjugates flourished). Two of the three cases of abundant occurrence of *Spirogyra* are from the deep pools at Dambulla, and this lends support to the view above suggested of the

* The relative scarcity of species of *Œdogonium* in the rock-pools may have something to do with the absence of a suitable substratum. The young plants tend to be epiphytes on other filamentous Algæ or on water-weeds; the only filamentous forms present are Conjugates, and these are well known to apparently afford an unsuitable substratum for epiphytes, whilst water-weeds are rarely present. In the pool at Hanwella the *Œdogonium* (*O. calcareum ?*) was attached to the rocky base, but this is the only example of the kind noticed. At Kurunegala there was a little of a water-weed growing in the rock-pool, and this bore the *Œdogonium* in this case; in another rook-pool at the same place many of the decomposing plant-portions forming a sediment at its bottom bore a fair number of 2- or 3-celled young plants of the genus in question.

efficacy of the dark rock-surface as a light-absorber and the consequent shaded character of the water in these deeper pools. The third case is from a pool at Kekirawa shaded by the neighbouring jungle. Of equal importance to *Spirogyra* are species of *Zygnema* which generally take its place; from no other waters in the island have I seen as much *Zygnema* as in the rock-pools. *Mougeotia* is completely absent, but in one case a considerable amount of *Gonatonema* occurred. In other cases filamentous Desmids (fig. 4, F and M) play a great part (species of *Desmidium, e.g., D. Aptogonium*, Bréb.,

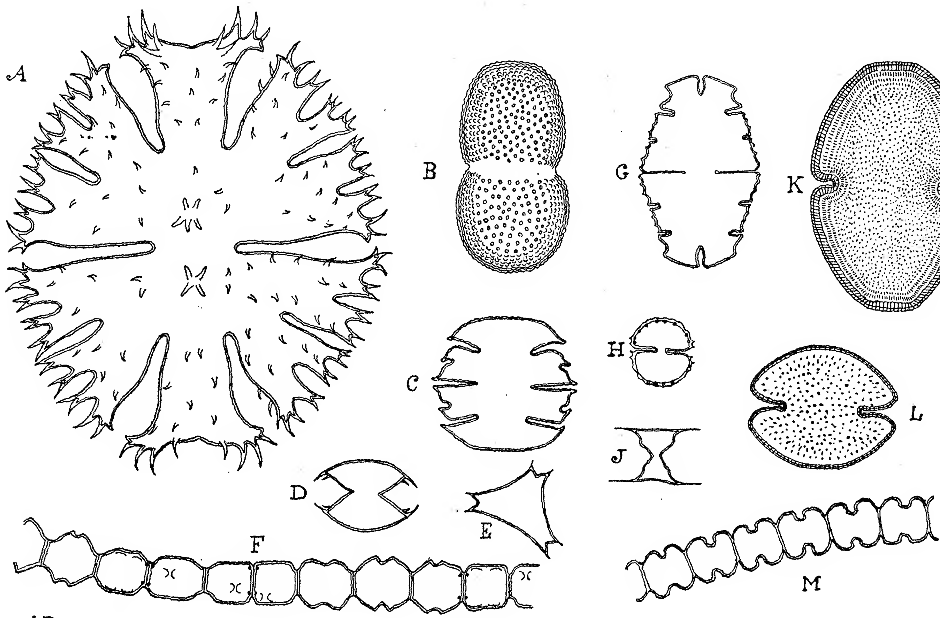


FIG. 4.—Illustration of the Types of Desmids characteristic of the Ceylon Rock-pools. The figures are intended to show the prevalent type, and in no way aim at giving an exhaustive representation of the great diversity of form presented by the Desmids of these pieces of water. A, *Micrasterias apiculata* (Ehrenb.), Menegh. var. (× 250). B, *Cosmarium decoratum*, West and West (× 250). C, *Micrasterias zeylanica*, n. sp. (× 250). D, *Staurastrum bifidum* (Ehrenb.), Bréb., side view (× 330 about). E, Ditto, end-view (× 330 about). F, *Desmidium quadratum*, Nordst. (× 330 about). G, *Euastrum zeylanicum*, n. sp. (× 560 about). H, *Cosmarium* (*cf. punctulatum*, Bréb.) (× 330 about). J, *Staurastrum aristiferum*, Ralfs? (× 330 about). K, *Cosmarium pseudo-pachydermum*, Nordst. (× 250). L, *Cosmarium Lundellii*, Delp. forma (× 250). M, *Sphærozosma secedens*, De Bary (× 560 about).

D. quadratum, Nordst., *D. didymum*, Corda, and *Sphærozosma, e.g., S. secedens*, De Bary). *Desmidium* is particularly characteristic of these pieces of water, while other filamentous Desmids (*e.g., Hyalotheca* and *Gymnozyga*) which are common enough in the ordinary lowland pools, are almost or completely

wanting. The unicellular Desmids show similar characteristic features; thus species of *Closterium* are either entirely absent or at least rare, and when present they are mostly not those species which are found in the other lowland pools; *Euastrum* is also much rarer than in the latter, but *E. dideltoides*, West and West and *E. zeylanicum*, n. sp.* (fig. 4, G) were rather abundant in one case. On the other hand, species of *Micrasterias*, which are rare in the ordinary pools, play a great part in these pieces of water (*e.g.*, *M. apiculata*, Menegh., *M. zeylanica*, n. sp.,† fig. 4, C, etc.), whilst species of *Staurastrum* (*e.g.*, *S. bifidum*, Bréb., *S. aristiferum*, Ralfs?) and *Cosmarium* (*C. decoratum*, West and West, *C. pseudopachydermum*, Nordst., *C. Lundellii*, Delp., *C. punctulatum*, Bréb.?) are strikingly abundant in contrast to their scarcity in the clayey pools. *Pleurotænium* (*P. Trabecula*) is sometimes to be found in some quantity. Looking at the Desmid-flora of the rock-pools in its entirety, one is struck by the complexity of form of the diverse species in contrast to the relatively simple forms assumed by the Desmids of the ordinary lowland pools. This feature is illustrated both by the unicellular and filamentous species (*cf.* figs. 3 and 4), and is certainly very noteworthy (possibly due to aeration of the water?) As already mentioned, numerous

* *Diagnosis.—Euastrum zeylanicum*, n. sp.:—Cells small, about one and a-half times longer than broad, very deeply constricted. Apical incision first slightly widened and then narrowed to more or less of a point. Semi-cells pyramidate, with pointed basal angles; apex convexo-truncate, the margin on either side of the apical incision being straight or slightly curved. Lateral margins with two incisions, of which the one next the apex is deeper than the other; upper portion of lateral margins (*i.e.*, part between the apex and the first lateral incision) retuse; portions of lateral margins between first and second incisions and between second incision and median sinus denticulate. Median sinus very narrow and closed, slightly dilated at its inner end. Cell-wall smooth. Zygospore not seen.

Length 45—50 μ, breadth 30—35 μ, breadth of apex 16—18 μ, breadth of isthmus, 8 μ.

E. zeylanicum has some points of resemblance to species like *E. radiatum*, Turn., and *E. serratum*, Josh., but the differences are perfectly obvious.

† *Diagnosis.—Micrasterias zeylanica*, n. sp.:—Cells small, length generally slightly exceeding the breadth, rather deeply constricted; sinus open, triangular acuminate with a pointed inner termination; semi-cells three-lobed, lobes separated by incisions, which penetrate as deeply as the sinus, and are inclined towards the latter; ends of terminal lobe bluntly pointed; lateral lobes with two blunt processes, separated by a narrow and rather shallow, rounded depression, the process next to the sinus being horizontal, the other bent down towards the sinus; polar lobe widely spreading, slightly drawn out at each extremity into a horizontal or deflected process; apex flatly convex. Outline very faintly granular. Cell-wall smooth or minutely punctate. Zygospore not seen.

Length 60—65 μ, breadth 55—60 μ, breadth of polar lobe 50—55 μ, breadth of isthmus, 15—18 μ.

Micrasterias zeylanica belongs to that group of species which includes *M. oscitans*, Ralfs, and *M. incisa*, Ralfs, but is more complex than either of these. In this respect it comes nearer to *M. truncata* (Corda), Bréb., which is, however, much more abundantly incised.

members of the Protococcales (*Scenedesmus*, *Pediastrum*, *Cœlastrum*, *Rhaphidium*, *Dimorphococcus*, etc.) sometimes accompany the Conjugate element in striking numbers, and in one or two cases Peridiniaceæ are quite common. The exceptional abundance of the flora in these rock-pools can only be referred to the high temperature of the water (perhaps also to the favourable conditions of aeration ?).*

Before concluding the description of the algal vegetation in the rock-pools, I wish to add a few remarks on the biology of the attached growth found on the rocky sides of these pools, and we may extend the discussion to the algal covering on submerged rock-surfaces in general. This attached growth is either an adhesive tangle or is composed of velvety tufts of pilæ. The former is often very compact, and consists either of a single species or more commonly of a number of closely interwoven forms. The basis in the latter case is generally blue-green, although green forms (*Œdogonium*, *Mougeotia*, *Microspora*, *Ulothrix*, *Stigeoclonium*) often make up a large part of the mass, whilst unicellular forms (Desmids, Diatoms, Protococcales) are frequently intermingled. Such adhesive tangles are, no doubt, composed of certain definite associations of species mutually dependent one upon another in certain respects, and extensive investigation would probably show that similar (in some cases perhaps identical) collections of species occur in different localities under the same influencing conditions. The advantage of such composite growth may lie in its forming a source of protection against the ravages of aquatic animals, but there may even be a more intimate relation involving the metabolic activities of the organisms concerned. For such associations of species I propose the term "*consortium*,"† one example of which has already been noticed in the *Lyngbya*-films found in Lakes Kantelai and Mineri (p. 227); *Pithophora*, with its associated epiphytes, may be mentioned as a second.‡ Consortia are, of course, to be found in every piece of water, and I hope at some later date to deal with those occurring in our waters.

* It may be suggested that the great specific diversity and relative individual complexity presented by the algal flora in these pools (and especially in the deeper ones) may be, to some extent, due to an absence of the external conditions influencing algal growth in other tropical pieces of water. Especially in deep rock-pools desiccation probably never takes place; the temperature is not subject to much daily variation; the aeration is probably fairly adequate; and the light conditions are not extreme. These characters of the habitat are probably favourable to the growth of a large number of different forms, whose vegetation goes on undisturbedly. A considerable amount of variation is thus possible in these waters, and I should not be surprised if a relatively large number of new forms will be found in them as a result of a more extensive investigation.

† *Consortium* (Latin) = fellowship, participation.

‡ *Cf.* Fritsch, "Problems in Aquatic Biology, etc.," 'New Phytol.,' vol. 5, No. 7, 1906,

The pilose growth (fig. 5), so often found coating rocky surfaces in the tropical fresh-waters, is almost entirely blue-green, and presents features analogous to those noticed above in connection with the subaërial flora. The pilæ consist of a single or of several different species, and in the latter case we are again dealing with a consortium in which the interrelation could be determined to some extent. In one of the rock-pools at Dambulla the whole submerged surface of the rock was thickly covered with such pilæ. When some of these were carefully scraped off, a dark dot was seen with the naked eye at the base of each of them. Microscopic examination showed that this dot was due to little radiating colonies of *Rivularia* (fig. 5, B and D), whilst the remainder of the pila was constituted by a species of *Hypheothrix*, the bundles of filaments of the latter arising from in between the threads of the basal *Rivularia*. The branched bundles of the *Hypheothrix* are held together to form the tuft by a very narrow species of *Oscillaria* ramifying in all directions between the bundles of *Hypheothrix*-filaments. In the outer portion of each pila there was a considerable amount of mud and decomposing algal substance, which afforded shelter to a number of green unicellular forms (*e.g.*, *Scenedesmus, Tetraedron*). The consortium here thus consists of a *Rivularia*, a *Hypheothrix*, and an *Oscillaria* with a few unicellular forms. It seems as though the *Rivularia* prepares the ground for the *Hypheothrix* which follows. A very similar pilose covering was found on the rocks in a small pond near the tank at Habarane, but the pilæ in this case were considerably longer. The basal *Rivularia* showed up very distinctly and, with a lens, its filaments could be seen radiating out in all directions (fig. 5, A). The species of *Hypheothrix* differed from the one observed at Dambulla, the filaments forming thick unbranched bundles, each constituting a single pila; as a result, there was no binding *Oscillaria* in this case. The slight differences, however, do not detract from the interest of the very considerable analogy. *Rivularia* plays a very important part in all the rock-pools, and in some of them was found growing on every conceivable object (including loose sediment).

As above mentioned (p. 228) the rocks round the edge of Lake Kantelai were covered by a thick pilose blue-green growth. This, again, consists of a species of *Hypheothrix*, the bundles of which are bound together by a delicate *Oscillaria*, but there is no basal *Rivularia* in this case. At the base of many of the pilæ a dark dot is indeed to be seen (fig. 5, C), but microscopic examina-

p. 157. Every piece of water contains forms, which are in part at least dependent one on the other, be it from the point of view of substratum, of shading, of transference to a suitable position in the water, or of protection from animal attacks: and all such associations of species occur together as a result of necessity.

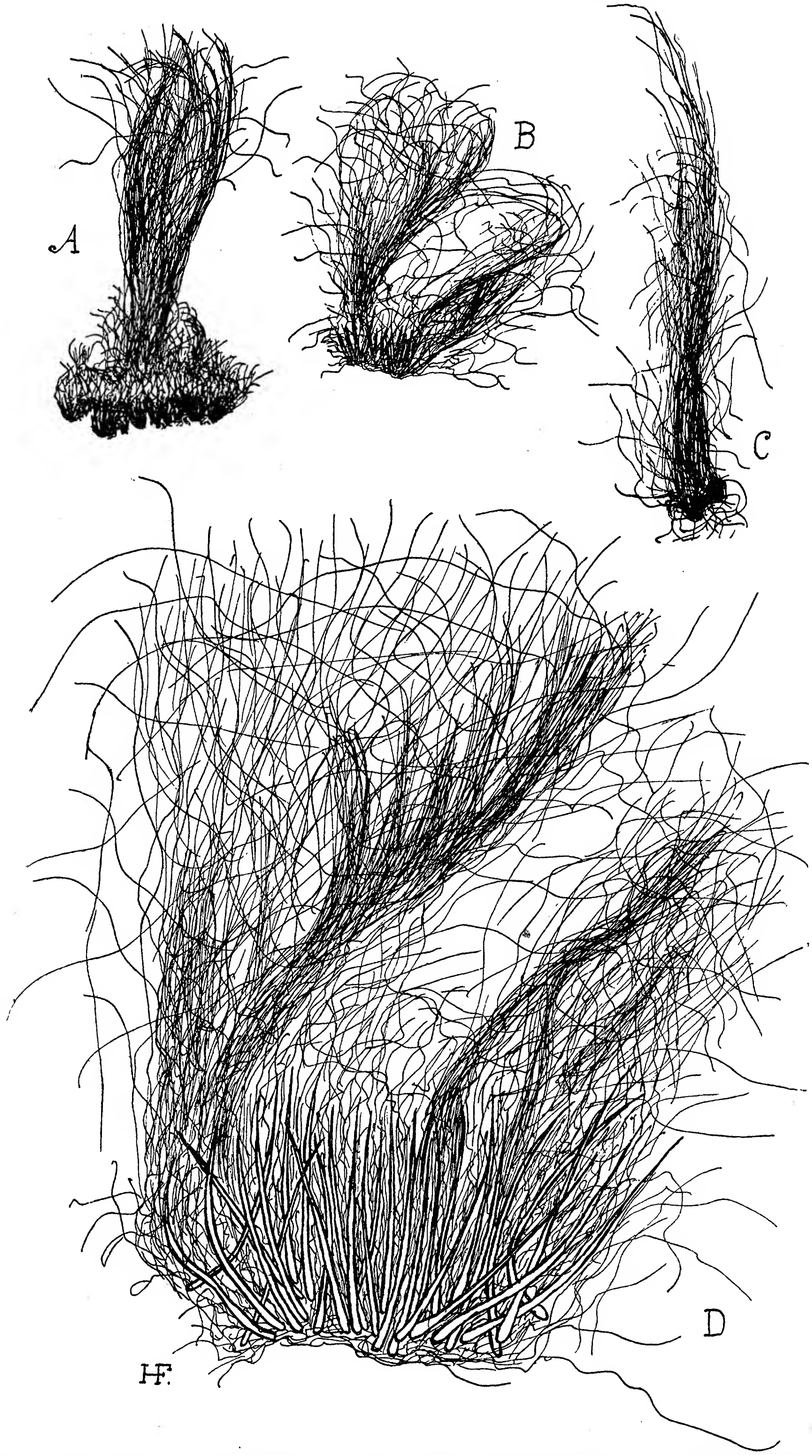


FIG. 5.—Illustration of Colonisation of Submerged Rock-surfaces. A ($\times 8\frac{3}{4}$), Single tuft from pilose growth on submerged rocks of a small pond near the tank at Habarane; growth of *Rivularia* at base of *Hypheothrix*. B ($\times 13\frac{1}{8}$), Single tuft from pilose growth on sides of rock-pools, Dambulla. D ($\times 35$), the same enlarged. C ($\times$ nearly 8), Tuft from pilose growth on submerged rocks in Lake Kantelai; the dark mass at the base is due to air. Full descriptions of all the figures in the text.

tion shows this to be due to a collection of air at these points. Pressure on the cover-glass breaks up this air into numerous small bubbles, which speedily become dispelled into the surrounding water, and after this process the black dot at the base of the pila has vanished. Perhaps we have here an air-bubble which was originally clinging to the rock-surface and formed the base for a growth of *Hypheothrix*, since some algal forms are occasionally to be found attached to the surface-film of air-bubbles in the water.*

In concluding the discussion of this subject, I should like to point out that blue-green Algæ in particular are noted for the frequent occurrence of dense collections of very diverse forms, which have been one of the most fruitful sources of the establishment of cases of so-called polymorphism. Had the observers who dealt with this subject attacked the physiological problems involved in these close associations of individuals, far more good would have been done than in the proclamation of cases of polymorphism on superficial data. For such collections of blue-green Algæ are certainly nothing more than highly interesting consortia.

(v) *Algæ of Wells and Springs* (*i.e.*, aerated but standing water).—I was only able to examine three examples of the algal growth in wells, but they have proved very instructive. The material is derived from three different localities (Nalande, Matale, and Ambalangodda), so it may be looked upon as fairly typical for the island. The fundamental point about these pieces of water is their good aeration. The water is generally at some considerable depth below the top of the well and is consequently not exposed to a very strong light, nor is its temperature probably in any way as high as in the more exposed waters we have previously discussed. The substratum is stone or wood work. The prevailing conditions are thus very marked and uniform and produce a very typical algal flora.

The predominant forms are species of *Pithophora*, which were present in all three cases and in two of them absolutely dominated the algal flora. In two of the three wells at least there was also a certain amount of other Cladophoraceæ (*Cladophora*, *Rhizoclonium*). Since the material was in all cases sterile and often covered with epiphytes, the discrimination of *Cladophora* and *Pithophora* was not easy; the large mass of the Cladophoraceæ present, however, showed the vegetative characters described by Wittrock† as characteristic of *Pithophora*. In two of the wells there was a certain amount of *Spirogyra* presenting the usual features, whilst blue-green forms (*Lyngbya*, *Oscillaria*) are always present, sometimes in quantity. *Œdogonium* was only

* *Cf.* also Fritsch, "The Structure and Development of the Young Plants in *Œdogonium*," 'Annals of Botany,' vol. 16, No. XLIII, 1902, p. 473.

† *Cf.* Wittrock, in 'Nov. Act. Reg. Soc. Sc. Upsala,' Ser. 3, 1877, p. 4.

observed in the well at Matale, where it occurred as an epiphyte on the *Pithophora*.

The only other forms of any importance are Diatoms, which were present in enormous numbers in two of the wells; in the third (at Ambalangodda) there were practically none, which is due, perhaps, to the main mass of algal growth found here being above water-level and consequently exposed to a higher temperature than in the other two cases. In the wells at Nalande and Matale the Diatoms occurred mainly as epiphytes on the *Pithophora;* in the former case there were epiphytic *Gomphonemas* and *Synedras* and loose floating tangles of *Fragilaria* (with intermingled blue-green forms and *Synedra*), whilst in the latter, except for a few *Synedras*, all the Diatoms were epiphytic (*Achnanthes*, *Gomphonema*, and *Synedra*). Nowhere else in the lowland fresh-waters was such a striking abundance of Diatoms observed, and I think this feature is here rather a result of the colder water than of the good conditions of aeration. *Fragilaria* is, however, a genus which prospers quite well in warm water (*cf.* below), and the conditions influencing its presence or absence are very unclear.

The vegetation of these wells is thus characterised by a Cladophoraceous and Diatomaceous element and shows a very uniform composition. The conditions are, of course, exceptionally favourable for Cladophoraceæ, for not only is the aeration adequate, but the lower temperature of the water involves a greater power of dissolving the necessary gases. The wells are just the kind of habitat in which we should expect to find Cladophoraceæ flourishing in the tropics (*cf.* p. 230), if anywhere. And their predominance in such waters furnishes, to my thinking, a striking confirmation of the causes suggested above for the scarcity of this order in other tropical fresh-waters.

A few words may be added on the vegetation of the hot springs at Kannia, near Trincomalie, although they will be dealt with more fully elsewhere. In hot springs we have aerated water at a high temperature, and this is the marked distinction between them and the wells. The springs at Kannia are roughly of two temperatures, viz., 37° C., and 40° to 41° C., and these two different temperatures appear to call forth an entirely distinct algal vegetation in the respective springs. Those at the higher temperature have the stone sides above and below water-level covered with a continuous tangled or filmy growth of blue-green Algæ (mainly *Lyngbya* and *Scytonema*), whilst the less hot springs (37° C.) have a brown, fluffy covering of *Fragilaria* on their sides. This difference is very well marked, especially as regards the *Fragilaria*, which scarcely appears at all in the hotter springs. Since there is no other obvious factor than the difference of temperature to explain this diversity, we

must look upon the higher temperature (only 4° C. above the other, however) as being the cause of the absence of *Fragilaria* in the hotter springs.

(vi) *Algal Vegetation in the Small Pools of the Uplands.*—The vegetation of the numerous small pools occurring round about Nuwara Eliya (especially on the so-called Moon Plains and along the route from Nuwara Eliya to Hakgalla) formed a ready means of study and furnished interesting materials for a comparison with the lowland pools. The differences are just what we should expect to find in view of the different conditions. As Mr. Nock kindly informed me, these small upland pools dry up for about a month during the dry period. Their water is generally almost quite clear, but stagnant, and the midday temperature (October 29) in four cases was found to be 19°·5 C. The bottom and sides in some cases seemed to consist of a white sandy loam, but in other cases they were clayey. Some of the pools are of considerable depth, others, again, shallow. Except for the slight shade afforded by the growth of neighbouring grasses, etc., the only protection from the strong light is found in the frequent occurrence of water-weeds, but some of the pools are quite destitute of such growth. The important conditions are the fairly low temperature, the clear water, and the probably rather intense illumination.

In very many of the pools the algal vegetation takes the form of a thin, almost transparent filmy growth covering the abundant water-weeds, and occasionally floating on the surface of the water. These films are so delicate that they break up as soon as one attempts to remove the weeds bearing them from the water, and the only way to collect them is to push the plants into the collecting-tube under water. This character of the films is due to their being composed almost entirely of unicellular forms, of which Desmids and a limited number of Protococcales are the most important. Algal growth of this kind is common enough in temperate regions,* and it is interesting to find it developed here, in this pseudo-temperate part of Ceylon; as far as I have seen, such films are not present in the lowland waters. A considerable part of the films is composed of mud and decaying organic particles, and this matter and the algal cells are no doubt held together to form a coherent whole by the considerable masses of mucilage† excreted by the Algæ forming the films. This mucilage is, however, very delicate, in most cases not being obvious without the help of stains, and this accounts for the very delicate and frangible nature of the films. Although films of this type have frequently been described, their origin has, as far as I am aware, not yet been

* *Cf.* Messrs. West and West, "A Monograph of the British Desmidiaceæ," vol. 1, Ray Society, 1904, p. 16.

† See especially B. Schröder, "Untersuchungen über Gallertbildungen der Algen," 'Verh. Nat.-Med. Ver.,' Heidelberg N. F., vol. 7, 1902, pp. 139—196, Plates VI and VII.

adequately explained. It may be noticed in this connection that the Desmids most involved are capable of slow movement with the help of the excreted mucilage,* and they probably tend to collect in considerable numbers on the surface of the water-weeds, attracted, perhaps, by the oxygen liberated during their assimilation. The prolific division of the Desmids thus established will soon lead to an accumulation of numerous individuals, whilst their mucilage-investments will flow together and form a whole. The frequent inclusion of Protococcales and of muddy particles in these films is not difficult to understand on this assumption, nor the occasional presence of Diatoms. Whether these composite films can be regarded as a true consortium must be left to further investigation.

Turning our attention now to the specific constitution of these films, we have, in the first place, to notice that the blue-green element is practically unrepresented; isolated filaments of *Oscillaria* are sometimes present, and in one case the films included a number of colonies of *Chroococcus*. As a rule, however, Cyanophyceæ are sought for in vain, and from this point of view alone these upland pools acquire an aspect rather distinct from those of the lowlands. The Desmids are the most important forms (species of *Cosmarium*, *Euastrum*, *Closterium*, *Micrasterias*, *Penium*, *Xanthidium*, *Pleurotænium*, etc.), but filamentous species of this group are exceptionally rare (only *Spondylosium*). This latter point is not difficult to understand in the case of the films, for here the absence of filamentous Desmids is probably due to the immobile character of these forms which, on the above assumption of the origin of the films, would be excluded from participation in their formation. A more puzzling feature, however, is the great scarcity of filamentous Desmids generally in the upland waters examined (*cf.* also p. 238, footnote). This is a second striking point of difference between the upland and lowland pools, for in the latter, where the conditions are favourable, filamentous Desmids are quite a prominent feature. It may be that the diversity is due to the different amounts of dissolved oxygen in the water in the two cases. We have only the analogy of the colonial Protococcales to go by, but in some of these (*Scenedesmus*, *Cœlastrum*) Senn† found that colonies were formed when there was a scarcity of oxygen, whereas an abundance of the latter led to the formation of isolated cells. Possibly, then, the conditions prevalent in the lowland pools are such as to favour the existence of filamentous Desmids, while in the uplands the reverse is the case. The lowland pools certainly afford striking examples of the filamentous tendency amongst the Desmids

* B. Schröder, *loc. cit.*, pp. 157—159, Plate VII, figs. 3, 4, and 10*a*.

† "Ueber einige koloniebildende einzellige Algen," 'Bot. Zeitung,' vol. 57, 1899, p. 97.

(*e.g.*, the occurrence of *Micrasterias foliacea*, one of the few forms of this genus that has assumed the filamentous condition). It is, of course, quite possible that there are other more obscure causes for the great scarcity of filamentous Desmids in the upland pools. With reference to the above suggestion, it may be pointed out that filamentous Desmids are, on the whole, also a rather rare feature in our waters (except *Hyalotheca dissiliens* (Sm.), Bréb., and *Gymnozyga moniliformis*, Ehrenb.), which may be due to the higher percentage of dissolved oxygen.

Of the unicellular Desmids, *Cosmarium*, *Euastrum*, and *Closterium* play the most important part in the composition of the films, one of these three being generally the dominant form. In some cases one or other of these three genera is almost alone represented, and we obtain a practically pure culture of a number of species of the respective genus. In other cases, however, the films show a more varied aspect, containing most of the Desmid genera above mentioned, though many of them only occur in subordinate amount. Some of the films are composed of Desmids only; in others various Protococcales (*Raphidium*, *Crucigenia*, *Cœlastrum*, *Eremosphæra*, *Scenedesmus*, etc.) play a more or less important part. No doubt the presence or absence of these latter forms depends on certain conditions—possibly on the quantity of organic substance dissolved in the water.* Diatoms occasionally occur in some quantity, but are often almost completely wanting.

The algal vegetation in the small pools of the uplands does not, however, always take the form of these films. In some cases one finds a granular or flocculose covering on the bottom, whose composition is quite identical to that of the films. A mass of filamentous green Algæ floating on the surface (*Spirogyra*, *Mougeotia*, *Ulothrix*, frequently associated with Desmids) is not very common. In a few cases various blue-green Algæ are found, mostly as a fluffy coating to weeds, etc. I was unable to determine whether they are only developed in particularly exposed localities. Lastly, I may mention that I met with a species of *Vaucheria* in the water of a small pool in the Hakgalla Botanic Gardens. This is the first record of a fresh-water species of *Vaucheria* from Ceylon.

Meagre as the facts thus are that I was able to derive from my brief study of the vegetation of these upland pools, they yet point to a marked diversity as compared with the lowlands and a distinct similarity to the algal flora of temperate regions. These facts point to the temperature of the water (and indirectly the lower percentage of dissolved oxygen) as one of the chief factors influencing tropical algal vegetation.

* *Cf.* Schmidle, "Aus der Chlorophyceen-Flora der Torfstiche zu Virnheim," 'Flora,' vol. 78, 1894, p. 64.